ESSENTIALS OF ZOOLOGY

ALEXANDER MEEK

ESSENTIALS OF ZOOLOGY

ESSENTIALS OF ZOOLOGY

FOR STUDENTS OF MEDICINE AND FIRST YEAR STUDENTS OF SCIENCE

BY

ALEXANDER MEEK, D.Sc.
PROFESSOR OF ZOOLOGY, UNIVERSITY OF DURHAM

WITH 145 ILLUSTRATIONS

LONGMANS, GREEN AND CO.
39 PATERNOSTER ROW, LONDON, E.C. 4
NEW YORK, TORONTO
BOMBAY, CALCUTTA AND MADRAS
1922

Made in Great Britain

PREFACE

Whether the student is to specialise in Medicine or Agriculture or is to pursue a course in Pure Science, his knowledge of Zoology must be founded upon and can only be obtained by personal enquiry with reference to a series of types. The types are selected with a view to his finding out for himself the more important facts of comparative anatomy, physiology and embryology, gaining practice in methods of study, and forming an acquaintance with the literature of the subject. These are the essentials, and should be conveyed by the teacher without undue bias as to the future studies of the student, and without particular reference to the problems which happen to be the fashion of the moment.

This work is arranged as a guide to the student in acquiring this essential fundamental knowledge. The types chosen are those used in the majority of the Universities and Schools, or are nearly allied to them. More are described than teachers have time usually to accomplish in the First Year; but in this respect it will meet the requirements of teachers who have the opportunity of adopting the recommendation of the General Medical Council that specialised instruction in Biology in its application to Medicine should be included in the medical curriculum.

The types are arranged in zoological sequence, and tables are given to indicate their systematic position. Nevertheless, the description of each is complete enough to permit the study commencing with reference to any one of them. The types selected, moreover, are generally distributed, or allied forms may be readily procured, so that the book may be used by students in other countries.

The illustrations are not meant to replace the drawings which the student will be required to make as records of his dissections and preparations. They are, on the whole, fresh and original. I have to thank my colleagues of the Zoology department of the University of Durham for help with some of them: Mr. A. D. Peacock, M.Sc., for figures 10, 11, 12, and the figures of the chapter on Insects; Miss Olga M. Jorgensen, M.Sc., for the illustrations to the chapter on Crustacea; Mr. F. W. Flattely, M.Sc., for figure 24; and Mr. B. Storrow, M.Sc., for figures 43 and 44. I have further to thank Mr. Peacock for help in reading the proofs.

ALEXANDER MEEK.

July 12*th*, 1922.

CONTENTS

ILLUSTRATIONS

ESSENTIALS OF ZOOLOGY

CHAPTER I

PROTOZOA

	Types
Phylum PROTOZOA	
Class RHIZOPODA (Sarcodina) . .	Amoeba
	Entamoeba
INFUSORIA—	
Sub-Class CILIATA . .	Paramecium
	Balantidium
	Opalina
	Vorticella
SUCTORIA	
FLAGELLATA (Mastigophora) .	Cercomonas
HAEMOFLAGELLATA . . .	Trypanosoma
SPOROZOA	Coccidium
	Monocystis
	Plasmodium

THE cell is the element of life. The tissues and the organs of the higher animals consist of or are derived from cells, and the Protozoa are one-celled animals or are simple colonies of similar cells. We therefore resolve the animal kingdom into the Protozoa, animals which are characterised by the cell being usually the individual, and the Metazoa, animals which consist of many cells more or less modified according to their position in the animal and the function they have to perform.

The same is true of plants. They occur in the one-celled state or in simple association and are grouped as Protophyta or Thallophyta, and, in a more complex, many-celled state, the

Metaphyta. Many of the groups of Protozoa and Protophyta are undoubted animals and plants respectively, but there are other simple organisms which, whether we view them from the standpoint of locomotion or method of feeding, or life history, or the nature of the cyst, if any, in which they are enclosed, cannot be satisfactorily relegated to either kingdom. The student will find that such are claimed both by Botanists and Zoologists. It is convenient therefore to think of a third division of these simple organisms, the Protista, for the reception of the primitive and lowly types which are not definitely animals or plants.

The cell is defined as consisting of protoplasm with a nucleus, and the nature of a free individual cell may be conveniently studied in one of the Protozoa, the Amoeba.

Amoeba.—In the warm months Amoeba may be procured from ponds with the help of a dipping tube or a fine net made of silk, from water tubs, from soil, and they may also be got at the shore. A drop of the water is placed on a microscope slide and covered with a covering glass. Examined with a low power at first, numbers of diatoms, desmids, and other Protophytes will be found with Metazoa as Rotifera, Crustacea, insect larvae and different kinds of Protozoa, many of them in active movement; but search should be made for a small, transparent, jelly-like creature, slowly moving in a peculiar and characteristic manner, during which the shape is being constantly changed. A close study of such a form will show that the Amoeba consists of a jelly-like substance in the midst of which is a small nucleus. The protoplasm of the nucleus has been called nucleoplasm, and the extra-nuclear plasm the cytoplasm. The distinction between the nucleus and cytoplasm becomes more apparent when the animal is killed with certain reagents, and especially if stained. The nucleus becomes plain; it stains readily and the cytoplasm does not.

In the living Amoeba the cytoplasm is clear and denser peripherally and is more fluid and granular internally, and may therefore be resolved into ectoplasm and endoplasm. But there appears to be little difference between the envelope of ectoplasm and the inner endoplasm except that the former is a surface film intervening between the plasm and the water.

The granular endoplasm contains round watery spaces called vacuoles, and some of them contain food in process of digestion and are called food vacuoles. In fresh-water conditions a special vacuole is seen which attains a large size and suddenly disappears, but only to reappear in the same place. This is the contractile vacuole. With the addition of dilute salt solution it gradually ceases to act, and an Amoeba from salt water may not, and usually does not, have a contractile vacuole at all.

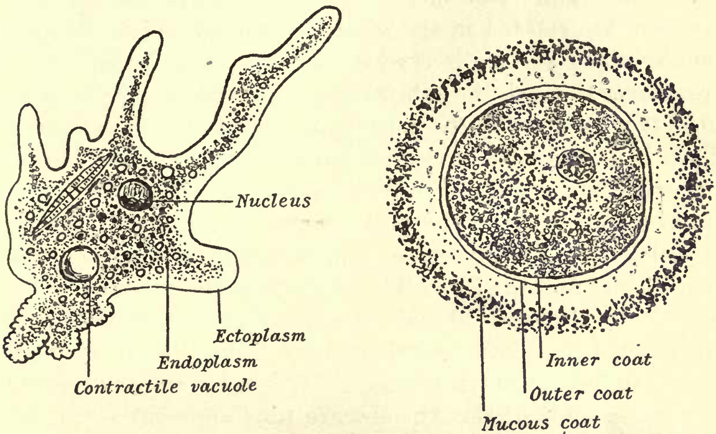


FIG. 1.—*Amoeba proteus*, free and encysted, the latter after Carter. In the former the movement is upwards and to the right. The pseudopodia are being produced anteriorly and are being withdrawn posteriorly. A diatom has been taken in as food, and food and other vacuoles are present in the endoplasm.

This goes to indicate that in fresh-water conditions the water imbibed through osmotic pressure tends to be excessive and has to be regularly discharged.[1]

Among the primitive granules which are so numerous in the endoplasm other granules may be observed of different form and size. According to their appearance and reaction these have been found to be either food particles reduced to a small state by digestive processes or products of an excretory nature. Small globules of fat have also been proved to be present in some cases.

[1] 1910. Zuelzer, *Archiv für Entwicklungsmech. der Organismen*, Bd. 29, p. 632.

It will be observed that the granules are in constant motion, streaming in currents along the cell in the direction of movement, and when a lobe of the ectoplasm is being protruded they suddenly pour into it and distend it. These lobes of the cytoplasm are called pseudopodia, and are produced freely in the water or in contact with a surface, so that in the latter case a sort of creeping movement results—amoeboid movement. In contact with a surface the Amoeba is thus translated in a given direction. Not merely the pseudopodia but the whole Amoeba are rotated in the direction of progression. A point on the upper surface is carried to the front end, and when it turns over to reach the substratum it adheres and is stationary until it is released by the passage of the rest of the cell over it. Then it is gradually carried over the posterior end to reach the upper surface again. The pseudopodia are by the movement brought into an ineffective position and are retracted, becoming crenulated in the process at the posterior end. The rolling movements and the formation of pseudopodia can be imitated exactly by drops of oil and even water in contact with fluids with which they form a surface film. Like the Amoeba, also, such can be made to change direction by suitable stimuli. The movements of the Amoeba are thus apparently produced by changes in the surface tension of the ectoplasm. But in the Amoeba the ectoplasm is contracted and expanded in a purposive manner, and pseudopodia are protruded without contact with a surface. Their near allies the Foraminifera produce long filamentous pseudopodia, extending far into the water as sensitive feeding organs. If the Amoeba be floating freely the contact of a pseudopodium with an object results in the Amoeba being pulled to the surface by the pseudopodium, which becomes sticky or thrombocytic, and this is followed by amoeboid movement along the object. The cytoplasm thus behaves as a colloid in a fluid state, and is limited externally in contact with the water as a film in surface tension, and it is occupied by vacuoles of watery fluid, also in a state of tension.

The pseudopodium is able to secrete a sticky substance which enables it to adhere to certain structures. This aids the movement, and it also helps in the ingestion of food, although experiment has shown that the food is not always fixed in this

way. There is reason to believe that in some species one part of the periphery may be specially endowed as a sort of mouth region. But what happens is that, when the diatom or other food has been encountered by the pseudopodium or pseudopodia, it is gradually surrounded by pseudopodial outgrowths, which, fusing together, bring about the lodgment of the food in the endoplasm ; this is ingestion. The food is now surrounded by endoplasm which secretes a watery fluid into the space occupied by the food, and if watched long enough the food will be found to be killed, broken up, and gradually dissolved. The undigested remains are got rid of by a reverse process which brings them to the surface ; this is egestion.

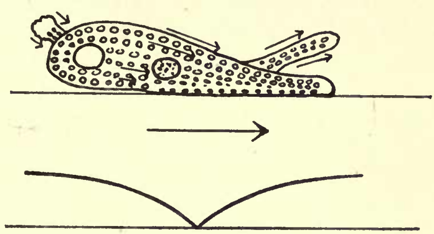


Fig. 2.—Diagram of the movement of an Amoeba, after Jennings. The upper figure indicates the relative rate of the granules and ectoplasm in the Amoeba and in the pseudopodia. The lower figure represents the path of a point on the surface.

The individual cell is thus able to move about, to take in solid food and digest it ; it is, in fact, able to live by the performance in a simple fashion of the ordinary physiological processes known to be essential to life.

Reproduction is very simple. The cell elongates, the nucleus divides into two nuclei, and these are carried apart in the elongating cytoplasm, which at the same time becomes constricted between them. The two halves finally become separated and two Amoebae are produced, each half the size of the original. In fresh-water conditions a new contractile vacuole appears in one of the daughter cells. These cells then proceed to feed and grow to the full size, when the process is repeated. The rate of growth and reproduction is influenced by temperature. Both processes are rapid in high temperatures and gradually become slower in decreasing conditions of temperature. Thus in temperate climates reproduction and growth are subject to a winter stasis from which there is a gradual change to a summer maximum of intensity.

After a period of multiplication it is believed, although it

has rarely been seen, that two Amoebae are attracted to one another, fuse, and as a result of the fusion a fresh series of ordinary reproduction divisions takes place. This process of fusion of two individuals is termed conjugation, or syngamy.

Encystment has been frequently observed. Provoked by some such external influence as advancing cold, drought, want of food, or probably occurring as a necessary rhythm of life, the Amoeba becomes spherical and secretes around itself a mucous coat within which first one and then a second thin coat is formed. Thus invested, it remains for a variable period, but usually about three months. In some cases the Amoeba appears to escape as it becomes encysted as a single Amoeba, but usually the nucleus undergoes fragmentation and a large number of small Amoebae is liberated.[1]

It will be noted that under ordinary conditions the Amoeba reproduces the same form with remarkable fidelity. But some degree of modification is possible under stress of conditions. One of these is encystment; another is the production of flagella. It has been demonstrated by Wilson that the soil Amoeba, which has been described under the name *Naegleria gruberi,* may become flagellated, that this state is assumed to escape rapidly from such bad conditions as too high a temperature or too intense light, and he was able to produce the change by adding distilled water to his cultures.[2] This method had already been followed by Wherry[3] in producing flagellates of soil Amoebae.

Wilson also found that the nucleus has a structure and undergoes processes during division which are remarkably similar to those of the cells of Metazoa. The stainable material of the resting nucleus is gathered into a part of the nucleus, forming a nucleolus or karyosome. When division is about to take place (prophase) the more firm or gel constituents of the nucleus are arranged in the shape of a spindle of eight fibres, which presents two opposite poles and an equator. The karyosome then becomes dumb-bell shaped and divides into two masses, which are attracted one to each of the poles. The

[1] 1915. Carter, *Proc. Roy. Phys. Soc., Edinburgh,* vol. 19.
[2] 1916. Wilson, *Univ. of California Publ. in Zoology,* vol. 16.
[3] 1913. Wherry, *Arch. f. Protistenkunde,* Bd. 30.

karyosome yields also eight small elongated bodies which are identified as chromosomes. The stainable products of the nucleus are thus the nucleolus and the chromosomes, together forming the chromatin.

The chromosomes occupy the equatorial region of the spindle and (anaphase) are constricted and divided transversely.

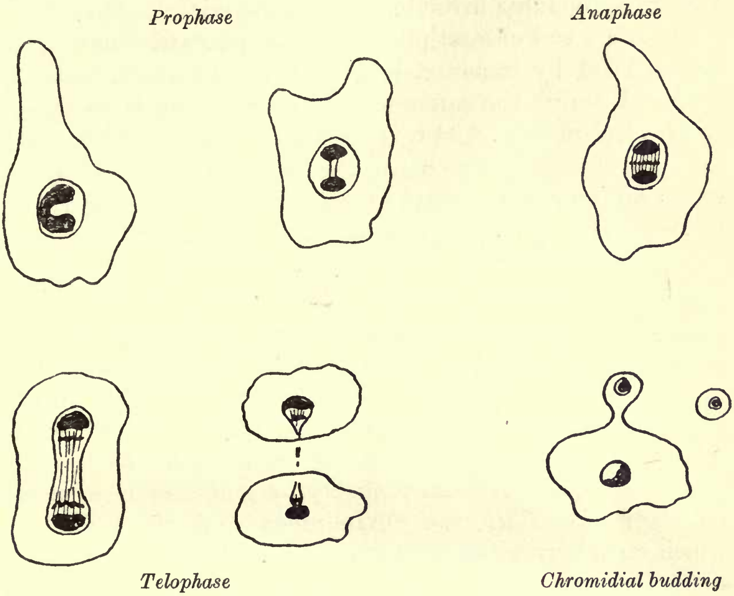


FIG. 3.—Reproduction of Amoeba. Mitotic phases of division, and reproduction by chromidial buds, after Wilson.

The resulting eight pairs of chromosomes migrate apart along the thread-like paths of the spindle.

During the migration of the chromosomes towards each pole the spindle elongates and (telophase the chromosomes are received into the respective polar areas already occupied by the halves of the nucleolus. In each area they are encircled to form the daughter nucleus and, the cytoplasm constricting along the plane of the equator, the two cells are separated. Dr. Mary J. Hogue [1] found that an Amoeba obtained from the oyster underwent the same changes during division.

In addition to this manner of cell division, which is so

[1] 1921. *American Jour. of Hygiene*, vol. 1.

common, especially in the growing stages of animals and plants, and is known as karyokinesis or mitosis, Wilson found that small masses of chromatin are given off from the nucleus. These are called chromidia and are liberated in bud-like outgrowths of the cytoplasm. This method of reproduction has been witnessed in other forms, and may be described as reproduction by budding involving nuclear material.

After a series of multiplication processes carried out by cell division and by budding, large numbers of descendants are produced during the summer when temperature is favourable and food plentiful. And it is possible in this case, as in others to be considered, that a change results from successive divisions which can only be remedied by conjugation or syngamy.

Amoebae are liable to desiccation, and in this state may be carried and widely dispersed by winds. They are also spread by streams and rivers and sea currents. It is not to be wondered at, therefore, that they are so widely distributed.

The Amoeba is very adaptable and fits well into its varied environment. All Amoebae have been derived from pre-existing Amoebae, and the survivors may be said to be the relatively unchanged descendants of all past ages. They represent a primitive and probably very ancient form of life, for their near allies, the Foraminifera and the Radiolaria, which form limy or siliceous skeletons, have been found in all geological formations from the beginning, and some of them form to-day a skeleton not very different from their predecessors of the Cambrian.

The Amoebae which are found even under the same conditions are not all exactly similar in form and structure. They differ in shape and in the form of the pseudopodia. The latter may be blunt and lobular, or they may be quite thin and pointed. We are not always certain that some of the changes are not due to differences in history under different conditions, that is, due to variation. But the differences have led to a number of species being described under the generic name Amoeba, as *Amoeba proteus*, *A. princeps*, *A. lobosa*, *A. limax*, and other species have been arranged under other generic names. These again are grouped under families, and the families are all brought together to form the order

Amoebaea. This order, with the orders Foraminifera, Heliozoa, and the Radiolaria, constitutes the class Rhizopoda of the Protozoa. This is the method universally adopted by systematists to arrange and classify the various kinds of animals.

Another large and important class is the Infusoria, which, instead of having pseudopodia or long filamentous extensions of the cytoplasm, are provided with numerous active, short, hair-like processes which are termed cilia. These Protozoa we may study with reference to two genera, Paramecium and Vorticella.

Paramecium, the slipper animalcule, is very common. It may be procured from stagnant water, rain tubs, fresh waters generally, and even from the sea. It is commonly found in infusions of hay and other vegetable matter.

The cell, which is the individual, consists of cytoplasm, and there are two nuclei, a macronucleus and a micronucleus. The cytoplasm is resolved into an internal endoplasm, granular and circulating like that of Amoeba, and an ectoplasm which is firm and forms a tough, elastic outer layer of characteristic shape. A special funnel-like depression leads to a mouth opening into the endoplasm. The whole surface, including the depression, is clothed with numerous fine cilia. The cilia by their combined action enable the animal to move about rapidly and freely, rotating on its axis, and their action in the neighbourhood of the vestibule and in the vestibule wafts food into the interior. The food is treated as in Amoeba, and the food and other vacuoles may be seen in the endoplasm. The two nuclei occur close together near to the vestibule, and there are two contractile vacuoles, one near each end.

It will be observed that Paramecium is long, somewhat blunt at one end and more pointed at the other. It moves almost in a straight line, but the movement is really a spiral one with the blunt end forwards and the mouth below. We may therefore speak of an oral or ventral surface, an adoral or dorsal surface, an anterior and a posterior end, and right and left sides. Polarity is thus strongly developed and manifested structurally.

It is clear that while the endoplasm is very similar in constitution and function to that of the Amoeba, the ectoplasm is a more definite, formed structure. It is a distinct membrane and is relatively impermeable, and it has been necessary therefore to provide an opening into it which acts as a mouth or entrance for the food. The opening consists

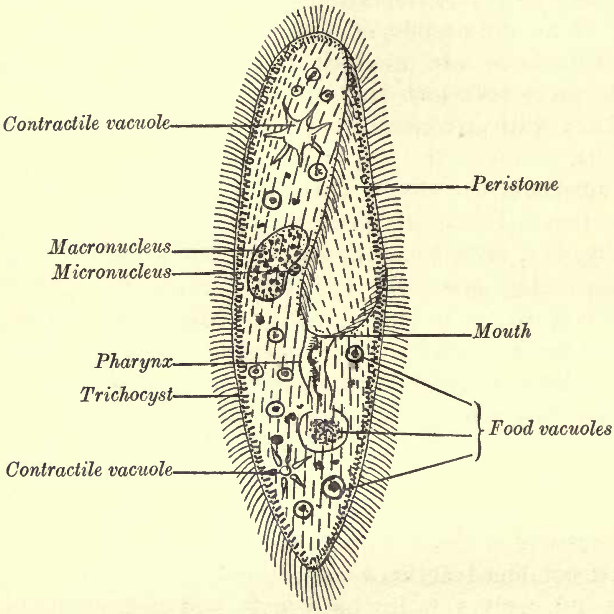


FIG. 4.—*Paramecium caudatum.* The oblique lines indicate the myonemes and also the rows of cilia associated with them. (After Bütschli.)

of a peristome, mouth, and pharynx, the last provided with an undulating membrane. It must be understood that while such popular terms are employed, they have no relationship to the terms employed with reference to the Metazoa, except that they refer to cell modifications which perform a similar function. To avoid them it has been suggested to call the mouth of such a modified cell the cytostome, and the cavity which leads from it to the opening into the endoplasm the cytopharynx. It has also been necessary to provide for the discharge of undigested material, and this is done in the case

of Paramecium by an opening, called the anus or cytopyge, to the exterior between the mouth and the posterior end. The contractile vacuoles when present, as they are universally in fresh-water examples, are also provided with pores. The ectoplasm bears the cilia. The cilia are free externally to the surface, but pass through the firm cortex to its inner surface, where they end each in a basal grain. The cortex is occupied by a series of minute sacs which open to the exterior. These are termed trichocysts and secrete a thread which can be shot out. In appearance the threads are very like the nematocyst threads of Hydra. They are believed to be protective, but in what manner and from what is not clear; they may be used to prevent the escape of prey. They may prove, in fact, to have a thrombocytic importance, and the thread to be one of mucin.

The internal surface of the cortical layer is striated by the presence of longitudinal bands, or myonemes. These are contractile and allow of contracting the cell and varying slightly its shape, especially when it is necessary to negotiate intricate passages amongst debris. In Paramecium the myonemes have a longitudinally oblique disposition. The superficial layer of cytoplasm in Paramecium, and the fact is generally true of the Ciliata, has been greatly modified to form a protective, sensory, locomotor covering to the cell.

Reproduction is regulated to a large extent by temperature. During a continuation of favourable conditions large numbers are formed by transverse fission. Both the nuclei divide and the remaining contractile vacuole is formed in each daughter cell. The macronucleus divides simply or without mitosis, but the micronucleus forms a spindle, and the chromatin gradually appearing is formed into chromosomes, which are divided transversely and migrate to the poles of the spindle. The nucleus is elongated during and after the migration of the chromosomes, and subsequently is constricted and divided. After a number of generations—about 170 in Paramecium—have been produced in this way it has been found that no further divisions take place until conjugation or syngamy of two individuals occurs. The two individuals fuse by the oral faces. The micronucleus divides by karyokinesis (mitosis) twice. Of the four resulting nuclei one only divides in each

Paramecium. Of these two nuclei, one in each migrates into the other Paramecium and fuses with the one which has not migrated. The remaining nuclei which have been formed during these changes, and the macronucleus in each case, all gradually disappear. The single nucleus in each Paramecium

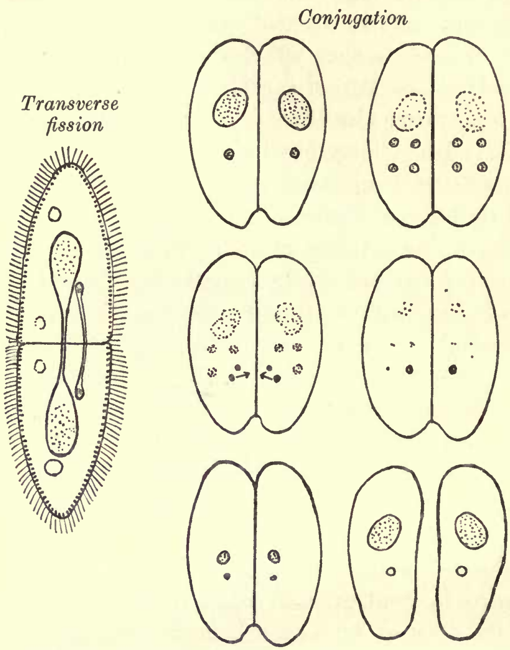


Fig. 5.—Reproduction of Paramecium. Diagrams to illustrate transverse fission and the nuclear changes which take place during conjugation. (After Delage and Hérouard.)

resulting from the fusion yields the micronucleus and the macronucleus after the process has been accomplished. Then the two Paramecia separate and begin a fresh series of transverse divisions.

Paramecium and other Ciliates have the power of encystment. The cell becomes rounded, the cilia are withdrawn, and the surface secretes a gelatinous substance which hardens. They are also liable to desiccation, and in such a state are carried with the dust and spread into other and sometimes, it

may be, very distant localities. The recognised species are widely distributed.

Vorticella, the bell animalcule, is common in fresh water, in marshes, and in the sea. It is similar to Paramecium essentially, but it is fixed by a stalk. The cell is modified into a bell-shaped expanded upper part or body, and a long stalk or peduncle which is firmly attached to plant or animal in the water. The bell consists of a granular fluid endoplasm containing a horseshoe-shaped macronucleus and a small rounded micronucleus, enclosed in a tough cortical ectoplasm, which is also continued into the stalk. A closer study will show that the bell ends in a rim or collar and that the free flattened end is occupied by a rounded flat disc separated from the collar by a groove, the whole forming the peristome. The cilia are compounded by fusion into strong membranellae and are restricted to the margin of the disc. The row overlaps to form a spiral, the outer limb of which is continued into a depression at one place. This is the outer opening of the vestibule which leads downwards to open into the endoplasm. It is provided with an undulating membrane produced by a further fusion of the cilia. The vestibule also provides a small opening for the discharge of undigested material remaining after the digestion of the food. As in Paramecium, there are therefore special openings for ingestion and egestion. The membranellae by their action set up a whirlpool-like current which attracts the particles of food in the neighbourhood into the peristome, and these are swept into the vestibule, and so to the endoplasm. The contractile vacuole discharges into the vestibule.

The cortical layer of cytoplasm is similar to that of Paramecium, but there are no trichocysts. There is a peripheral layer which covers the cell completely and the peduncle. Internal to this are numerous myonemes which are disposed in longitudinal direction, but there are besides several circular myonemes, especially around the collar. The whole cortical layer, in fact, is a highly modified part of the cytoplasm to provide a sensory surface and intimately associated contractile fibres, the myonemes. The longitudinal

myonemes are produced at the base of the bell to form a spirally directed contractile filament which ends in the adhesive disc of the peduncle. The peduncle thus consists of

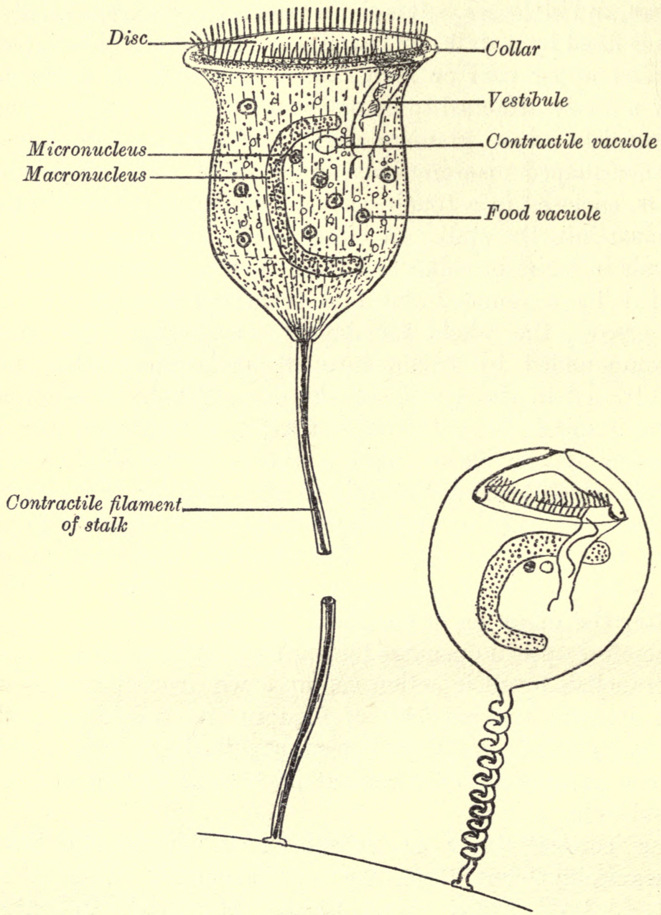


FIG. 6.—Diagrams of Vorticella in the expanded and contracted state.

a cortical layer and a central filament. Vorticella responds readily to movements conveyed through the water. The disc is withdrawn and covered by the contracted collar, and the peduncle is shortened by being thrown into a spiral. It is

able thus to retreat among the stalked diatoms and other organisms which find a foothold in the same region. When the disturbance has ceased it gradually advances again, the peduncle becoming straight and the bell expanding.

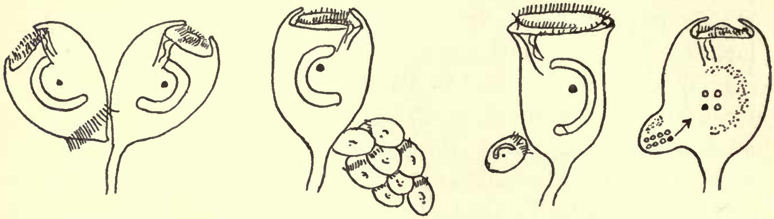
Should the region become untenable from such causes as lack of food, the bell portion of the cell develops a basal ring of cilia and detaches itself from the peduncle. Thus freed it swims away—the disc is the forward end—to seek another situation, where it becomes attached and renews its fixed life. It settles down by the base, the basal cilia are withdrawn, and a fresh stalk is developed by an outgrowth of the base of the cell.

On the other hand, a cyst may be formed, and in this case, as in the others, the body is rounded, the cilia withdrawn, and the ectoplasm in spite of its differentiation is reduced to a relatively simple condition.

Reproduction is effected in a manner very similar to that of Paramecium. Cell division takes place by the two nuclei dividing and the cytoplasm being split longitudinally from the middle of the disc to the base. One of the daughter cells retains its hold of the peduncle. The other develops a basal ring of cilia and becomes separated. After a period of freedom it settles down and develops a stalk from the basal end of the cell.

After a number of such divisions have occurred, a change sets in which brings the process to an end. When this last division of the series takes place one of the individuals resulting undergoes a succession of fissions, thus forming a cluster of small individuals, the microzooids. These are detached and become active swimmers in search of a stalked individual which is in a state demanding conjugation and is able to attract the microzooid. The microgamete, as we may now term the small individual, settles down at the base of the macrogamete and fusion takes place, only the cortical layer of the microgamete being discarded. The micronucleus of the microgamete divides three times and that of the macrogamete twice, and one of the resulting nuclei in each case divides again. One of the two nuclei resulting fuses with one of the other, all the rest disappearing. The nucleus derived

from the conjugation divides successively to form eight nuclei. Seven of these are macronuclei and the eighth divides to form the corresponding micronuclei, when the seven individuals



Fission *Formation of microzooids* *Conjugation*

FIG. 7.—Reproduction of Vorticella. The diagrams illustrate fission, the formation of the microzooids, and the fusion of a microzooid with a stalked Vorticella.

separate and commence a fresh series of ordinary divisions. But reconstruction after conjugation is variable, even in the same species.

Colonial forms allied to Vorticella are also common. They result from longitudinal fission involving a part of the stalk, the individuals remaining together, e.g. *Epistylis*, *Carchesium*, *Zoothamnium*. Such colonial vorticellids will be found to be very common.

Many flagellate Protozoa, usually called monads, will have been seen by the student while looking for the types described above. They illustrate another modification of the individual cell and are nearly always very small. Almost any of these free forms will show the active spiral movements produced by the one or the two whip-like processes with which the simple cell is furnished. The contractile processes are called flagella, and usually spring from one pole of the cell. The protoplasmic body is very simple, consisting of cytoplasm containing a single nucleus, vacuoles, and frequently a contractile vacuole. The ectoplasm is very thin. Of these Flagellata some are plants, some animals, and some are to be regarded as protists, while others may be stages in the life-history of Flagellata and other Protozoa. CERCOMONAS is interesting, for it may become lobed posteriorly by amoeboid extension of the cytoplasm. This organism is common in fresh water and in

infusions. It possesses a single anterior flagellum, and the posterior pole is pointed and may be produced into a long appendage, and, as has been said, this pole may present pseudopodial processes as well. The latter are formed usually as a preparation for conjugation. Reproduction takes place by longitudinal fission, and after a season conjugation takes place by equal-sized individuals, and such are termed isogametes. Mastigamoeba and its allies are still more intermediate in character between the amoeboid and flagellate Protozoa.

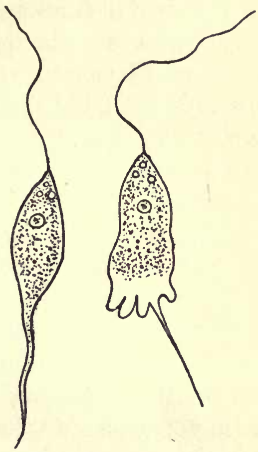


Fig. 8. — Cercomonas, after Stein. The flagellum is anterior, and the tail process and the pseudopodia posterior.

General Considerations relating to the Protozoa.—The cell may be studied from several different but related aspects. It has a form and structure which are reproduced with great constancy generation after generation. It has a form which can be defined; it can be compared with other forms of cells and the structures which determine the form specified. This study constitutes Morphology; in this case cell morphology. The cell is living, and life is manifested by movements and processes the study of which in Protozoa and Metazoa is called Physiology. During its life, moreover, the cell responds to stimuli of various kinds, and in the free state exhibits a behaviour with respect to these the study of which lies in the domain of Psychology.

Morphology.—It has been said that the living cell has a form and a structure which are apparently constant, but we have already seen that in addition to the living protoplasm there are food constituents and waste materials, that water is essential, and that a certain amount of change is constantly taking place connected with the liberation of energy and the building-up processes necessary to compensate for the loss.

Material is taken up and is being discharged, and these processes are accompanied by the gain and loss of energy. These considerations lead to a deeper enquiry into the constitution of the cell, its chemical composition and physical state. Chemically, protoplasm is regarded as a mixture of highly complex carbon compounds—carbon combined with nitrogen, hydrogen, and oxygen, with iron, sulphur, and phosphorus—in a colloidal state. From the examples we have studied it is evident that physically the colloids are resolved into a more or less firm gel and a sol containing granules. The ectoplasm of Amoeba is an incipient gel, a gel which becomes more distinct in Flagellata and especially in Infusoria. The endoplasm is a sol, it behaves as a sol, and is in a constant state of metabolic fluctuation. Turgidity is produced by water which distends the ectoplasmic skeleton of the cell, and the water associated with protoplasm may be regarded as water of colloidisation. Water is present also in vacuoles, and in some cells to such an extent as to reduce the protoplasm to threads of extreme tenuity. It is probable that the cell sap of the vacuoles only is lost in desiccation. The vacuoles are in a state of surface tension, and between them the protoplasm is constantly streaming in the spaces at its disposal. It has been noted already that in addition to water carrying material in solution, other inclusions may be found in protoplasm.

The nucleus is similar, but it may be looked upon as an assemblage of colloids of somewhat different composition, which forms a membrane in contact with the cytoplasm, the nuclear membrane. It is a fluid which is the medium of important chemical changes. It may give rise to a framework of linin, and it contains or may produce a substance characterised by its staining properties and called chromatin. The chromatin is carefully divided during cell division, and this manifestation of mitosis has naturally led to the conclusion that the chromatin transmits thereby inherited qualities. At present, however, it is just as well to observe that the whole cell is carefully orientated during division, and that the whole plasm, cyto- as well as nuclear, is divided.

Ordinary chemical analysis does not indicate the differences in the composition of the protoplasm from different sources,

and it is evident also that precipitated protoplasm is not the same as living protoplasm. But bacteriological methods, experiments with drugs, and haemolytic and other reactions have demonstrated that it is specific and even individual in peculiarity.

The condition of the water in which the cell lives, with respect to salinity, density, temperature, and viscosity, determines the volume and the shape of the cell and the intensity of the physiological processes. The volume tends to increase in fresh water and to contract with increased salinity, and this is associated with osmotic pressure. These conditions have also an influence on the rate of action, and even the presence of the contractile vacuole. The shape of the cell may be altered with change in temperature and the associated change in viscosity. The accumulation of products of decomposition acts detrimentally on some Protozoa and encourages others. Thus Biochemistry and Biophysics have arisen as sciences of importance which are rendering welcome help to the morphologist, the physiologist, and even the psychologist.

Physiology.—Multiplication is periodic, and after each event the cell starts from half size and grows to full size. It is clear then that the food material, some of it, is converted into living protoplasm. In all the Protozoa which we have examined the food may be observed in the process of being ingested and the undigested remains egested. The endoplasm provides vacuoles in which it undergoes changes. The food as such disappears, and we feel from what we observe with regard to growth that it is being digested and dissolved in the process. It follows that the contact of the food with the endoplasm provokes the secretion of enzymes or ferments capable of killing, breaking up and dissolving the food. It has been demonstrated, in fact, that the first enzymotic action is accomplished in an acid state, and the subsequent ones in an alkaline state. The digestion then is quite similar to that which takes place on a larger scale in the higher animals. In the case of the cell, digestion and absorption are necessarily intracellular. The enzymotic fluids secreted by the protoplasm first reduce the food to a simple, soluble condition, and then reassemble it to suit the constitution of the

protoplasm, and it is gradually built up into, and takes its place in, the colloid material of the living cell. During its progress from the state of food to living material it may be oxidised to provide the energy required in carrying on the life processes. The residue represents the material available for growth. This goes on until full growth is being approached, when an equilibrium is reached between digestive capacity and the energy required, and this is the prelude to cell division. It is evident that in a state of encystment enzymotic action is practically suspended together with nitrogenous consumption; the small amount of energy required in this state of inanition is contributed by the oxidation of the protoplasm.

These changes so characteristic of life are called metabolic changes (metabolism), the building-up processes associated with enzymotic action are called anabolic (anabolism), and the breaking-down processes mainly associated with oxidation, katabolic (katabolism). The anabolic processes are directly related to the digestive processes and the presence of secretions, and the katabolic to the development of material, some of which may be used as loci for the development of higher compounds, but most of which is deleterious and has to be discharged as excretion. Excretion should not be confused with egestion.

The oxygen dissolved in the water is essential to the life of the Protozoa, for the energy derived from the food is brought into use by oxidation, and it has been proved by experiment that Protozoa cannot live in water from which oxygen has been removed. Carbon dioxide is a common product of oxidation in all cells, and with other similar products is easily passed out of the cells at the surface in exchange for oxygen, and this is respiration.

The Protozoa lead a simple life and exhibit in their life an epitome of the essential physiological processes. They behave as animals; that is, they are holozoic. The energy they obtain and utilise is probably in the main derived from food. The Protophyta obtain energy from the sun's rays in holophytic existence, and otherwise the group exhibits a wonderful capacity of forming enzymes in response to different kinds

of food in saprophytic and parasitic conditions, and of freeing energy by enzymotic action, even in the absence of oxygen.[1]

Psychology.—The Protozoa are nervous. Vorticella in the fixed state is irritable and contractile. In response to waves communicated by the medium in which it lives a contraction at once takes place, involving the bell and the stalk. Some part therefore of the cortex of the bell, or all of it, is capable of receiving the waves, but evidently the peristome is particularly sensitive, and the effect is transmitted to the myonemes and the contractile filament of the peduncle. There in are, other words, a sensory receptor surface and a primitive neuromuscular system intimately associated. With respect to Ciliates and Flagellates in general, we can point to modifications of the ectoplasm concerned in the process. The reflex in the case of Vorticella is protective and is automatic, and may be said therefore to be instinctive. It results with unfailing regularity when disturbance takes place, but it varies in quantity. The contraction may not be quite complete, and the length of the contraction varies. This means that the cell is able to inhibit both the contraction and the expansion.

But this is not all. Vorticella is able to develop a special band of cilia and to snap itself free from the peduncle when conditions become difficult or impossible. This is a postponed reflex associated with the presence of, or the ability to form, a breaking joint. It may be said that this postponed reflex, like the other, is provoked in response to external stimulus; but it points also to volition, and its history to a gradual modification of the cytoplasm in association with protection.

It is difficult for us to appreciate the meaning of all this. Experiment has shown that such free cells are attracted or repelled by various stimuli. From the results of experiments they are described as being positively or negatively phototactic, chemiotactic—that is, attracted or repelled by light or chemical stimuli—and so on. The impression conveyed is that the cell is like a boat without men, directed and controlled by wireless waves. Many Protozoa alternate between periods of desiccation and a free and usually an aquatic life. In the

[1] 1915. Bayliss, *Principles of General Physiology.*

latter state the Protozoon is subject to rhythms of growth, encystment and reproduction. Apart from the encystment and the desiccation, it is constantly working for a living, and under normal conditions it is found in so many diverse situations, with reference to depth, light, and other factors, that we are led to conclude that it is not merely the victim of circumstance but is volitional. It is attracted or repelled by heat, cold, and other influences. It moves, however, not only in response to external stimuli, but of its own accord, and even if the feeling be only a dim, incipient one, chemical and physical changes communicated by the cell sap, we might be inclined to say that Vorticella is aware when it is hungry and when it is contracted or expanded, and that all are conscious of their periods of movement and rest.[1]

These considerations apply to the individual. There are other studies which concern the race, the assemblage of the individuals which constitute a more or less complete group.

Reproduction.—It is interesting to find among the Protozoa evidences of sex. After a number of ordinary cell divisions a change takes place which is expressed in the tendency to fuse in pairs. It is still more striking when the conjugating cells are different in size, as in Vorticella. The cell after the conjugation passes through a number of phases of growth and division, and observation goes to show that normally the number is approximately the same for each species, and when this number has been accomplished no further multiplication in this manner can take place until conjugation has been effected. It is evident, for one thing, that the fusion occurs by a chemical attraction between the gametes. If the chemical difference is initiated at the first division after conjugation and becomes more and more intense at the subsequent divisions, and finally becomes sexual, then about an equal number of male and female gametes will occur.

The phenomena of division and conjugation have been followed for the most part in certain Ciliates and in parasitic Protozoa, and it is evident from the succession of events that the nucleus is the centre of the changes which occur. In

[1] 1904. Jennings, *Behaviour of Lower Organisms.* Carnegie Institution of Washington.

the Ciliates during conjugation the nucleus undergoes an elaborate series of divisions, and of the products only one belonging to each gamete migrates and fuses with another belonging to the other gamete; all the others are absorbed. The cytoplasm does not appear to suffer much change, and in Paramecium, after the nuclear reduction has occurred, the conjugating individuals separate and the original cytoplasm and its orientation are adopted. Moreover, during the phases of growth and cell division which follow, the cytoplasm is divided, together with the nuclei, and the polarity expressed by the cytoplasm is carefully preserved.

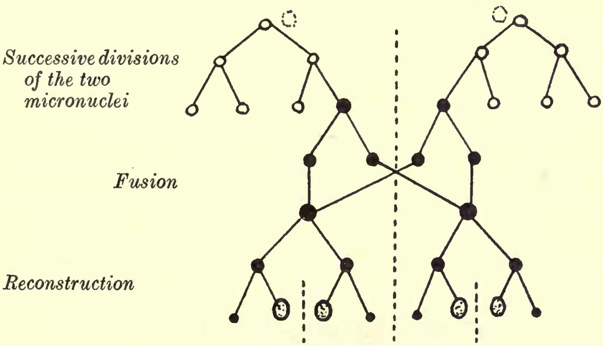


FIG. 9.—Diagram to illustrate the nuclear changes during the conjugation of Paramecium. The nuclei which disappear are shown by circles, the surviving nuclei by shading.

Conjugation is by no means universal. Certain of the primitive Protozoa have found a means of adjustment without it, and in many lowly examples chromatin material either has not been found or has a transient appearance. But the more modified Protozoa have become so specialised as to accumulate chemical differences during cell divisions which have to be neutralised by conjugation.

Distribution.—Attention has already been directed to the wide dispersion of Protozoa by wind and current. They form an important part of the floating life (plankton) of fresh waters and the sea, and many species occur in both. In consequence the monographs which have been published on Protozoa may be used for the identification of gatherings of plankton almost anywhere. The student who wishes to pursue the subject in

this direction may consult Ward and Whipple's 'Fresh Water Biology,' Cash's 'Ray Society Monograph of the British Rhizopoda,' Saville Kent's 'Manual of the Infusoria,' and special works like 'Nordisches Plankton.'

Symbiosis.—Protozoa and minute algae are sometimes associated, with mutual benefit. In such an association, the Protozoon is relieved of its waste material and supplied with oxygen, and the alga is provided with all the food it requires, including carbon dioxide, and it enjoys the protection furnished by the cytoplasm of the Protozoon. Such an association mutually beneficial is expressed by the word symbiosis.

Parasitic Protozoa.—All of the groups of Protozoa are liable to a temporary, accidental appearance in the alimentary canal of higher animals. Many are destroyed by the digestive juices, but some are able to survive and to pass through the alimentary system without much change. A number have found it possible to live and multiply in the alimentary canal as facultative parasites, and others have become adapted to living in the Metazoa and have changed into obligatory parasites.

Examples of these will be met with in the course of dissection of the types which follow, and others are of a high degree of importance from the diseases which they produce in man and mammals.

Amoebaea.—An amoeba called *Entamoeba histolytica* has been found in the intestine of man when affected by tropical dysentery. It has an amoeba-like appearance, possesses a small nucleus, and reproduces by fission and the formation of chromidial buds. Several kinds have been described.

Ciliata.—Only one or two ciliates have been found in association with disease; *Balantidium coli* has been obtained from the intestine of man and of the pig. OPALINA is common with accidental visitors in the large intestine of the frog. Opalina is ciliated, has a thin ectoplasm with longitudinal myonemes and several nuclei; there are no food nor contractile vacuoles, no mouth opening. These negative characters are associated with the food of the parasite being imbibed from the food of the host. Opalina reproduces by transverse fission

and leaves the frog in the encysted condition. The cyst yields many small spores, which if swallowed by tadpoles grow into the adult Opalina found in the frog.

Sporozoa.—A large number of parasitic Protozoa are grouped under this title, and are better known as gregarines and coccidia. A common coccidium affects the liver of the rabbit. It causes a white-spotted condition of the liver, and the disease is called coccidiosis ; this species is *Coccidium oviformis.* Coccidiosis is common in all vertebrates, and coccidia are found in several invertebrates.

Gregarines are found only in certain invertebrates and in Ascidia, not in any of the higher classes.

Monocystis.—The gregarines may be illustrated by Monocystis, the spore masses of which are so common in the seminal vesicles of the earthworm. In describing the history of such parasites as Monocystis it has been found convenient to introduce the term Trophozoite for the members of the trophic or feeding phase, and Sporozoite for those resulting from spore formation.

The Monocystis trophozoite is a single elongated cell with a small nucleus. It inhabits the mother cell which produces the sperms of the earthworm and grows there by imbibing the juices. When it is fully grown it escapes and is now a gametocyte. Two individuals come together and a mutual cyst is formed about them. The nucleus in each divides to form a large number of nuclei arranged peripherally, and they are freed with cytoplasmic investments. Fusion takes place among these cells or gametes in pairs, and it is evident that the pairs arise respectively from the two original cells, for they colour differently in Leishman's stain. The cell resulting from the fusion is invested in a spore case and divides to form eight sporozoites. How these are spread is not known.

Plasmodium.—Plasmodium (Haemamoeba), the cause of malaria in man, and its allies are parasites of the blood corpuscles of vertebrates and are spread by invertebrates. They are necessarily very small. The trophozoite phase of Plasmodium is a small amoebiform cell which, entering a red corpuscle, feeds and grows until it practically fills the corpuscle. A vacuole is present during the early growth, but it gradually

degenerates and finally disappears. When the trophozoite is fully grown it contains granules of pigment. It becomes rounded; the nucleus splits up into a large number of nuclei, which are liberated with a share of the cytoplasm. These

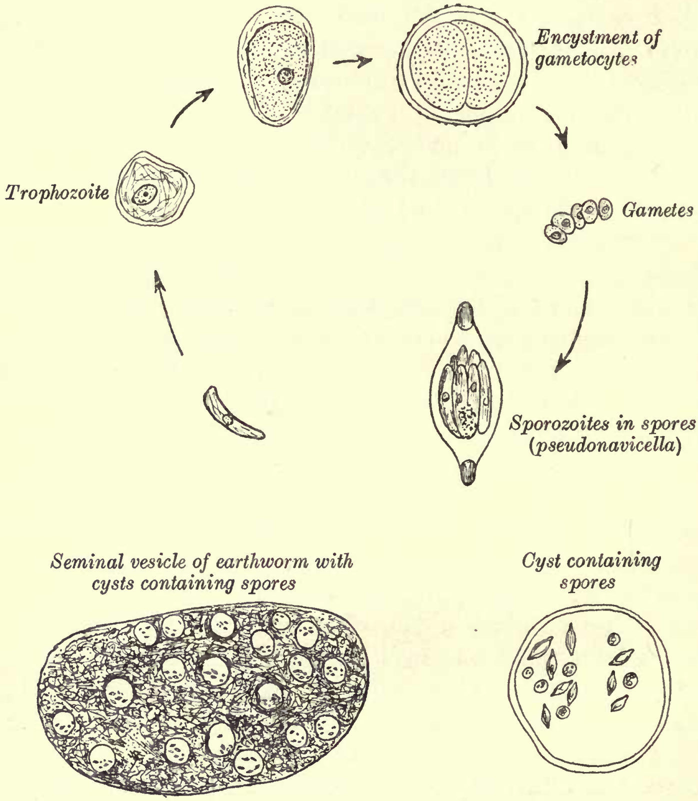


FIG. 10.—Monocystis. Diagrams illustrating life-history.

invade other red corpuscles or are destroyed with the broken-up corpuscles by the leucocytes of the blood. Such cycles are repeated several times, and this phase of the life-history is called that of schizogony. It is followed by a sexual change. The fully grown Plasmodium becomes oval in shape and then crescentic, and male and female crescents can be distinguished by certain characters.

The further development of these takes place in the mosquito, a blood-sucking insect. When the blood is received into the alimentary canal of the insect the crescentic shape

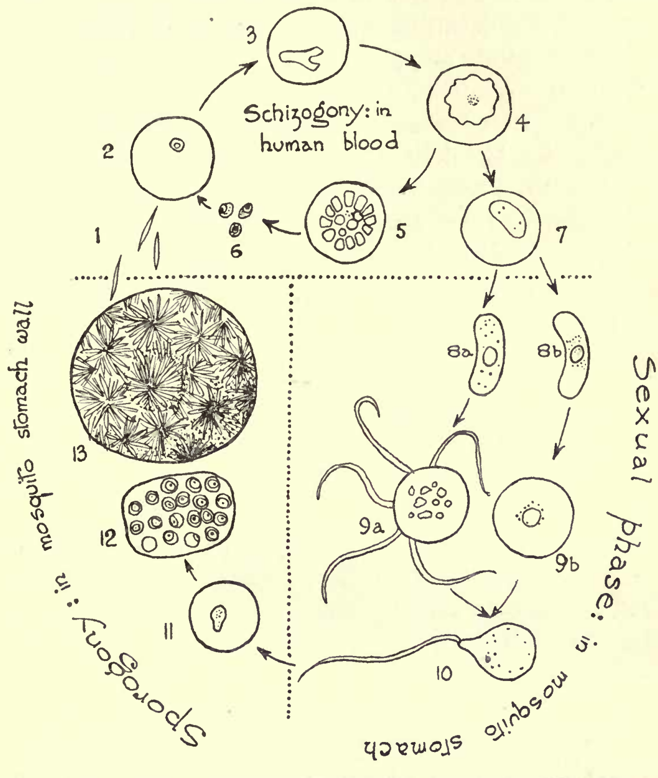


FIG. 11.—Plasmodium. Diagram illustrating life-history, after Minchin and the British Museum models. 1, sporozoite; 2–4, growth of sporozoite after entering red blood corpuscle; 5, breaking up into sixteen merozoites; 6, merozoites; 7, the Plasmodium becoming a gametocyte; 8a, 9a and 8b, 9b, male and female gametes—the changes which occur in the female gametocyte in producing the gamete are not shown; 10, conjugation of male and female gametes to form zygote; 11, zygote in stomach wall of mosquito; 12, spore mother cells in cyst in stomach wall of mosquito; 13, cyst containing ripe sporozoites.

changes into a rounded one. The male cells yield each four to six chromidia, which migrate to the surface of the cytoplasm, and a corresponding number of filiform microgametes are produced and liberated. The female cells mature by the

formation of two polar bodies. Conjugation takes place, and a zygote is formed which elongates and pierces the stomach epithelium, beneath which it becomes encysted. The encysted cell grows and the nucleus followed by the cytoplasm divides, and the resulting cells are termed sporoblasts. The sporoblasts multiply next, producing a large number of minute nuclei which migrate to the surface, become associated with cytoplasmic processes and are freed as sporozoites. These escape into the blood sinuses of the insect and are spread all over the body, finally reaching the salivary glands. In the salivary glands they are very small filiform bodies. This phase of life is that of sporogony. When inoculated to man by the insect they penetrate the red cells and begin the trophozoite phase.

Should the sex cells formed in man at the end of schizogony not find their way to the mosquito, the female members of the series may develop parthenogenetically—that is to say, without fertilisation—and thus produce a fresh outbreak of the trophozoites, it may be years after the original infection took place.

Plasmodium is therefore holoparasitic, and alternates between man and the mosquito, feeding and multiplying by schizogony in man and undergoing conjugation and a great multiplication by sporogony in the mosquito. Beginning as a parasite in the ancestors of the nearly allied insects concerned, it became adapted to the conditions of existence in the blood of the hosts used by these insects to obtain their food by blood-sucking. It is evident that the disease cannot be spread except by the insect.

Plasmodium appears to be restricted to gnats and mosquitoes of the dipterous Insect family, Culicidae. The feeding hosts of Plasmodium are man, anthropoid and other monkeys, other mammals, and lizards and snakes.

Haemoflagellata.—Flagellate Protozoa are very common in the alimentary canal of Metazoa, and some of them have become highly specialised and often pathogenic. Trypanosoma is found in the blood of Vertebrates, and in the case of two species is the cause of sleeping sickness in man. The cell

is elongated and consists of a granular endoplasm and a thin ectoplasm. The ectoplasm is produced to form a fine undulating membrane ending in a flagellum. The ectoplasm of the flagellum is differentiated to form a band which runs along the edge of the undulating membrane to end in a body called the blepharoblast. Near this is a nucleus-like body called the kinetonucleus or parabasal body. A nucleus is also present, and to distinguish it from the kinetonucleus it has been called the trophonucleus. The parasite progresses by the action of the flagellum, which is posterior. Schizogony takes place in the blood of the vertebrate host, and some kind

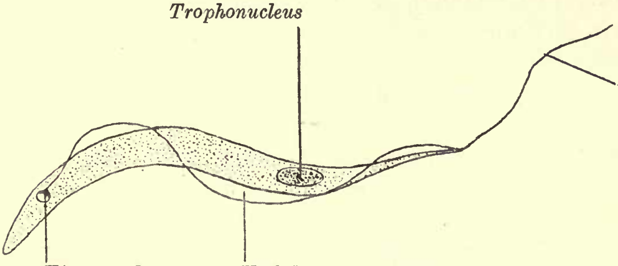


FIG. 12.—Trypanosome.

of sex development is supposed to occur in the invertebrate blood-sucker. In the case of the Trypanosome, which causes sleeping sickness, the insect host is the tse-tse fly. With relation to sleeping sickness, two species of tse-tse flies and two species of Trypanosomes have been described—*Glossina palpalis* and *Trypanosoma gambiense* and *G. morsitans* and *T. rhodesiense.* The genus Trypanosoma and its allies are widely distributed in vertebrates, including fishes, marine and fresh-water, and the invertebrate hosts are also varied. Trypanosomes, moreover, appear in some cases to be confined to invertebrate hosts.

In consequence of the importance of the diseases involved, Protozoology, like Bacteriology, has come to occupy a prominent place in Medicine.

CHAPTER II

COELENTERATA

THE Protozoa are regarded as forming a phylum of the Animal Kingdom. The Metazoa are resolved into a series of phyla, and each phylum is divided into classes, orders, families, genera, and species.

The phylum Porifera—sponges—may be said to belong to the Metazoa; some regard the sponges as allied to the Coelenterata, and others are of the opinion that they are an independent offshoot of the Protozoa.

	Types
Phylum COELENTERATA	
Class HYDROZOA	Hydra
	Obelia
CTENOPHORA	
SCYPHOZOA	
ACTINOZOA	

Under the name Coelenterata are included Hydra and its allies in fresh water, and marine Zoophytes (Hydrozoa); also jelly fish (Scyphozoa) and sea anemones and corals (Actinozoa). Ctenophores are mostly planktonic jelly-fish-like organisms allied to Hydrozoa and to the Planaria.

The characteristic features of the class Hydrozoa and of the Coelenterates are well illustrated by the fresh-water polyp, Hydra, and its allies the zoophytes found in the sea.

Hydra.—There are three species of the fresh-water Hydra: *Hydra vulgaris*, colourless, spread apparently over all the world; *H. fusca* (*oligactis*), brown or reddish in colour, common all over the northern hemisphere, and rare to the south; *H. viridis*, green, also common in the northern hemisphere,

but not extending so far to the south as the brown Hydra. They are found attached to weeds, in ponds and lakes, and in quiet streams and rivers.

Hydra has a cylindrical body, and the free end is surrounded by a number of tentacles. The structure of the body is simple. It consists of a double sac made up of many cells closely adpressed. The outer layer is called the ectoderm, and the

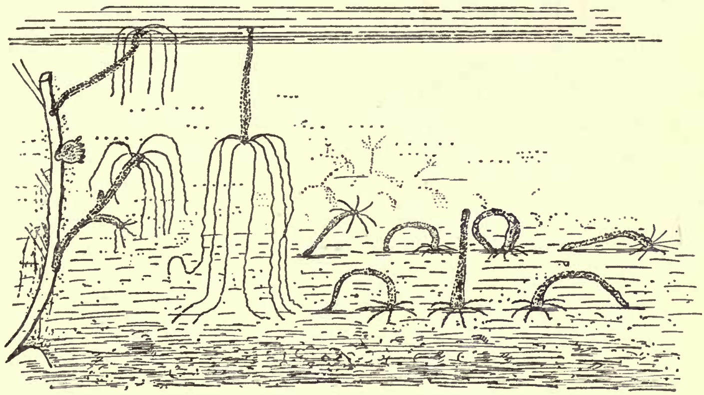


FIG. 13.—Hydra, after Trembley. On the left, attached to a twig, Hydra is seen in the expanded state and budding, in the retracted state, and in the act of attaching the tentacles to the surface film. By releasing the base and applying it to the surface of the water it becomes suspended from the surface as shown. The succession of figures to the right illustrate in the background rapid movement by looping, and in the front still more rapid progression by somersaulting.

inner layer the endoderm. The two layers are continuous at the mouth opening, which is situated at the free end of the body. The mouth leads into a central cavity bounded by the endoderm, and the cavity is called the gastric cavity, or enteron. The structure is that of the gastrula, a stage in development passed through by all the Metazoa. The gastrula marks therefore an important event in the evolutionary history of all kinds of Metazoa (phylogeny), as it does in the embryological history of each individual (ontogeny). There are allies of Hydra, as Microhydra, found in fresh and brackish water, which are without tentacles, and thus have a typical gastrula structure. Hydra departs from the structure in

that processes of the body wall are developed which act as grasping organs or tentacles.

Hydra is irritable and contractile. The body when fully expanded is about $\frac{1}{4}$ in. long, and the tentacles may be produced to a greater length, becoming fine and filamentous. Both the body and the tentacles when the animal is disturbed are retracted, the body to a small knob and the tentacles almost to the point of disappearance. The result in the case of the many-celled Metazoon, Hydra, is thus very similar to that of the Protozoon, Vorticella. In the undisturbed, expanded state Hydra is able to capture food, which is introduced to the mouth by the tentacles, and so to the gastric cavity or enteron where it is digested. In this state also it is able to move by gliding along upon the cells which form the base of attachment or pedal disc, and which then develop pseudopodia. Quicker movements are produced by the animal looping like a caterpillar with the aid of the tentacles, the cells of which may also develop pseudopodia, or even by somersaulting the base over the temporary fixation obtained by the tentacles. They may quit their hold of the weed and attach themselves by the base to the surface of the water. Rarely they quit their hold and float freely in the water.[1]

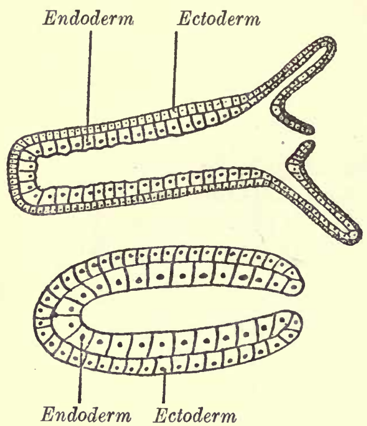


FIG. 14.—Diagram of general structure of Hydra and of a gastrula.

The Hydra may thus externally be resolved into a basal disc, a body or column, a ring of tentacles, a projecting cone bearing the mouth and termed the hypostome. From the above it is already obvious that a section of the body, or of one of the tentacles, is essentially the same. The section

[1] 1744. Trembley, *Mém. pour serv. à l'Hist. d'un genre de Polypes d'eau douce.*

presents a ring of ectoderm and a ring of endoderm, between which there is a third supporting layer mutually secreted between the adposed faces of the two layers. This layer, the mesogloea, is not formed of cells.

The **Ectoderm** is protective and nervous, and a closer study of sections will show that the cells, though apparently all very similar, are modified for various purposes. The layer is made up mainly of cells, columnar in shape, but broader externally. They form a columnar epithelium which is flattened on the hypostome. Externally they define the general surface of the body, and the exposed cytoplasm of each presents a distinct ectoplasm. They gradually taper towards the mesogloea, against which layer they expand into one, or sometimes two or three processes which are directed longitudinally. Externally these cells are sensory and internally contractile; they are not merely protective, they are neuromuscular. Certain cells, moreover, have become especially nervous. Such will be seen near or applied to the mesogloea and recognised by their small size, large nucleus, and the fine processes which proceed from them. These processes are nerve fibres, and are formed into a network coming into close association with the contractile filaments of the epithelial cells. They are thus associated with bringing about a concerted action in the contraction of the body.

Generally distributed likewise, and only slightly different from the general neuromuscular cells, are cells which are glandular, and secrete a substance of the nature of mucin. Practically all the cells of the basal disc are of this nature. Between the epithelial cells at their bases are numbers of small cells which are called interstitial cells. These may replace all the others, are especially concerned with reproduction, and give rise to a third type of cell which is eminently characteristic of the Coelenterata, the stinging cell. Stinging cells are common on the tentacles, where they occur in groups or batteries, and in the upper part of the column.

The stinging cell or nettle cell—nematoblast or cnidoblast—consists of a cell in the form of a cup within which is produced a capsule containing fluid. The external wall of the capsule is infolded into the capsule as a long spirally coiled

D

thread. The cell itself is otherwise simple ; it has a nucleus, and the cytoplasm projects at one point of the margin as a process termed the cnidocil. The cnidocil is irritable, and when touched it is able to set up a compression aided probably by an influx of water resulting in the expulsion of the thread, which in the process is turned outside in. The process may be readily observed by adding a little dilute acetic acid to the water containing the Hydra. If the effect be watched under the microscope it will be found that there are two kinds of cnidoblasts. One has a long thread which is shot out with sufficient force to be penetrating, and the thread is armed by barbs at the base. This is the poisonous or stinging cell proper, and its function is not only to help in securing the prey but to paralyse it. The other has a shorter and thicker thread which even in the free condition assumes a spiral disposition, and it is unarmed. Its purpose is to wrap itself round the prey, or a part of it, and thus to prevent its escape.

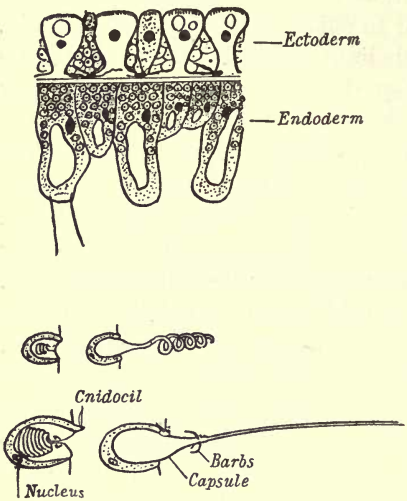


FIG. 15.—Section of body wall of Hydra. In the ectoderm the ectodermal cells often present vacuoles, and are separated at the base by interstitial cells. This region is occupied also by nerve cells. The endoderm cells are occupied by numerous zoochlorellae. Below are shown the two types of stinging cells.

Endoderm.—The endoderm is practically colourless in *H. vulgaris,* it is brown in *H. fusca,* and green in *H. viridis.* The column of endoderm thus stands out prominently in the coloured species in contrast with the colourless ectoderm. Sections will show that the endoderm cells are arranged as an epithelium bounding the gastric cavity. They are larger than the epithelial cells of the ectoderm, and are either flagellate or amoeboid on the inner or free border. The brown colour of

the brown Hydra is said to be due to small particles of an excretory nature accumulated at the base of the endoderm. In the green Hydra this region of the endoderm is occupied by green cells of an alga called Zoochlorella, a green alga which in this case, as in some Protozoa and other lowly Metazoa, is able to resist digestion and to live symbiotically within the animal cell, as the allied Xanthella does in so many marine Coelenterates and Protozoa. In the endoderm of Hydra the algal cells obtain protection and the food they require. Hydra is relieved of excretory material, and the carbon dioxide liberated by the animal is split up by the plant, the carbon utilised by the alga, and the oxygen by Hydra.

Many cells of the endoderm of the hypostome are glandular, and these contribute during the ingestion of food to maintaining a digestive activity of the watery fluid of the enteric cavity, and the ferments of the fluid of the gastric cavity release the food from the hard cases of small Crustacea and the like, which are ejected in the entire state but robbed of the digestible contents. When the food is introduced into the gastric cavity it is disturbed by the lashing movements of the flagella. This action brings the food into the requisite position, and then the flagella are withdrawn and pseudopodial extrusions are produced for the purpose of bringing the food within the endoderm cells. Digestion is completed, therefore, intracellularly. Food vacuoles are formed, and the digestion proceeds as in a Protozoon. When the food is reduced by fermentative action to a fluid state it is distributed by osmotic currents to neighbouring cells, and it must evidently pass through the mesogloea to gain the cells of the ectoderm. The undigested remains of the food are egested through the mouth. The food consists of small Crustacea and young Crustacea, insect larvae, and worms.

The general physiological processes of Hydra are very similar to and but little advanced beyond those of the Protozoon. The differentiation into a protective, sensory ectoderm and a digestive layer shows a division of labour, expressed by morphological change. It is evident also that the ectoderm is supplied with food by the endoderm ; there is no circulatory

system, but nevertheless currents carry the digested food from the endoderm through the mesogloea to the ectoderm. It has been shown by experiment that a starving Hydra may lose mouth and tentacles, a remarkable result of the cessation of, or the reversion of, the osmotic current—an indication also of a return to a simpler condition. In each cell the food obtained in a fluid state is reassembled by further enzymotic action to suit the condition of the cell, and in each it is liable to oxidation in the production of work. Both the ectoderm and the endoderm are highly contractile.

Psychologically the condition of Hydra is a lowly one. The cells are undoubtedly related by contact in a nervous manner, the epithelial cells by protoplasmic threads probably, and besides a generalised nervous system is outlined. The cells, however, in their processes and in their reactions are to a large extent independent. Local contraction is also manifested in the bending of the body and of a tentacle.

Reproduction.—Owing to the small degree of specialisation and the universal presence of the two layers in all parts of the column and tentacles, Hydra regenerates readily from sections. Cut in two, the lower half of the body reproduces the head and the upper half the base, and in all cases the original orientation is preserved. This was described in 1744 by Trembley,[1] but his statement that the Hydra could be turned inside out, and that the ectoderm became the new endoderm and the endoderm the ectoderm, is not believed, and experiments of the same kind have not been followed by this result.

Fission may take place either horizontally or vertically, but this method of vegetative reproduction has not been often observed.

During the summer, when food is plentiful, growth takes place rapidly, and new individuals are produced by hollow buds emerging from the side of the column. A bulging-out takes place of the two layers, and the bud grows as a new column and forms a mouth and tentacles at the free end. A secondary bud may appear before the new hydra is freed. The separation takes place by the base of the daughter hydra

[1] *loc. cit.*

constricting. The budded hydra floats away from the parent, and new individuals are thus produced and liberated in great numbers.

Sex cells are formed usually at the approach of winter. Some individuals are, or appear to be, practically males, but the usual condition is that sperm cells and ova are formed in succession in the ectoderm of the same individual. The interstitial cells are the seat of origin in each case.

Near the tentacular region of the column one or several groups of interstitial cells begin to divide, forming in this way a large number of cells distending the epithelium cells about them into a cone-like hump, called the testis. At the end of the period of cell division the cells become converted into flagellate spermatozoa, which are liberated through an opening at the summit of the cone-shaped swelling.

Lower down the column, and usually, as has been said, at a later period, a group of interstitial cells yields an ovum which grows by developing pseudopodia and feeding upon the other interstitial cells. A swelling styled the ovary is thus produced, which projects out as a tumour on the side of the column.

When fully grown the ovum becomes rounded in the cavity containing it, and two polar bodies are budded off from its outer surface ; thereafter the egg pushes its way through the ectodermal cells of the ovary and, anchored by these cells, projects into the water. Spermatozoa are attracted by the ovum and, one of them gaining admission, fertilisation takes place. The ovum then divides repeatedly and a sphere of a single layer of cells is produced. This stage of development is called the blastula, and the cavity is called the segmentation cavity. The inner face of the single layer of cells buds off cells which are to form the endoderm. These do not arise from a definite region of the outer layer, but generally ; they are said therefore to have a multipolar origin. At the same time the ectoderm secretes a coat of mucus on its outer face, and this is the prelude to the formation of two protective coats, an outer horny shell and a more delicate membrane internal to it. The process also involves the separation of the embryo from the parent column and it falls to the bottom.

At this stage, then, the embryo consists of an ectoderm and endodermal cells protected by a double envelope. The outer layer of the case may be roughened by spiny processes. In this condition the embryo may remain many months. In temperate regions the eggs are formed on the approach of winter, and thus the protected embryos are carried over the cold months of the year. They lie in the mud during the winter in a dormant state, and are called to further development with the coming of warmer conditions in the spring.

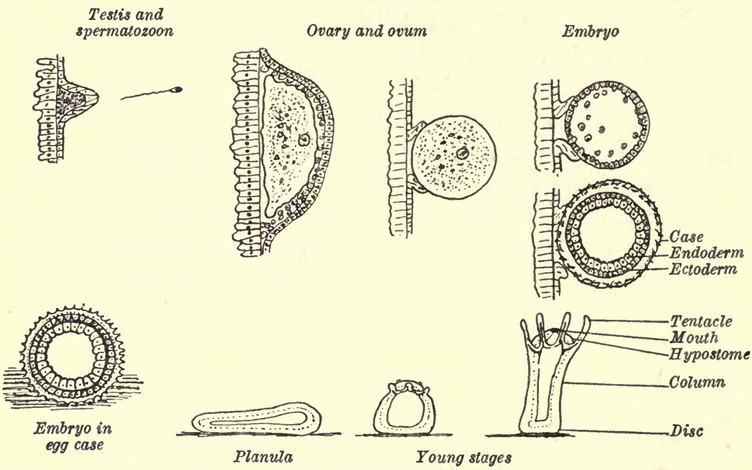


FIG. 16.—The reproductive cells of Hydra and stages in development.

During this period, however, Hydra is liable to be widely dispersed by river currents, and the egg cases may be desiccated and carried by winds.

Before the winter rest takes place the embryo usually is a two-layered one, the endoderm having formed itself into a layer on the inner face of the ectoderm. A mesogloea is secreted between the two, and interstitial cells are formed. In the spring, and in tropical conditions on the coming of the wet season, the embryo escapes from the shell as a two-layered larva or planula and creeps forward by an end which may be called the anterior one. It finally settles down by the anterior end and develops tentacles and a mouth at the opposite pole.

Although the endoderm arises without reference to a definite pole, it is thus evident that polarity is established, and there is every reason for believing that the animal pole of the egg, that from which the polar bodies are liberated, is the anterior pole of the planula larva and the pole of fixation.

Some of the near allies of Hydra use their tentacles for creeping movements and move about freely. An expansion of the body in the region of the tentacles converts the body into an umbrella shape, and thus a primitive medusa is produced, which has been called an actinula. The actinula is able to swim, and thus an alternation between a creeping or fixed state and a pelagic state has been found in fresh-water forms nearly allied to Hydra.

Further information will be found in papers by Brauer (1891, 'Zeitsch. für wissensch. Zool.' Bd. 3; 1909, 'Zool. Anz.' Bd. 33), Chun (1892, Bronn's 'Klass. und Ord. d. Thierreichs,' Bd. 2), Potts (1906, 'Quart. Jour. Micro. Science,' vol. 50).

A flattened infusorian, *Trichodina pediculus*, may sometimes be seen creeping over Hydra when it is being examined in the living state. It does not appear to produce any harm to its host. Martin [1] pointed out that in the lochs of Scotland Hydra is liable to attack by the Planarian, Microstomum. Hydra is eaten also by insect larvae.

Obelia.—Hydrozoa are very common in the sea, and shore species may be procured readily for examination in the living state. They are usually colonial forms, and they are usually also protected in a case secreted from the ectoderm, and anchored firmly by root-like outgrowths of the base. These compound hydroids are practically confined to the sea, but the genus Cordylophora is common in rivers and canals of the northern hemisphere.

Obelia is chosen for particular study, for the genus is world-wide in distribution and the species are common at the shore. *Obelia geniculata* is practically cosmopolitan in distribution: it extends from tropical to temperate and cold seas of both hemispheres. The hydroid is attached to stones,

[1] 1908. *Quart. Jour. Micro. Science,* vol. 52.

wood, sometimes to Crustacea, but is especially common on the fronds of Laminaria near low-water mark. The colonies are fixed to the alga by branching roots from which the stems project freely into the water. If one of the colonies, or a portion of it, be removed and placed in a watch glass with sea water the general features of structure will be easily made out.

The colonial structure is obtained by the fixed part growing out in various directions on the substratum, and the stems growing out therefrom freely and branching into a series of zooids provided with mouth and tentacles. The whole structure is protected by a sheath secreted by the ectoderm. That part of the colony which is attached to the substratum is called the stolon or hydrorhiza, and the free part the stem or hydrocaulus. The investing chitinous sheath is termed the perisarc, and the hydroid body which it invests the coenosarc.

The chitinous tube covers the branches of the stolon, and these end blindly. On the stem the sheath is directed in a succession of loops which give a characteristic zigzag appearance to the stems. The short branches of the perisarc are ringed at the base, and end in vase-like cups termed hydrothecae or calycles, and each cup is widely open.

The coenosarc of the stolon also ends blindly at the end of each of the rooting branches, but in the stem, while it provides a common body continuous with that of the stolon, it expands in each hydrotheca into a zooid provided with mouth and tentacles. These have been called the polypes or nutritive zooids. The zooid is occupied at the summit by a wide mouth. Between this and the ring of tentacles is the hypostome. Below the ring of tentacles the cup contains a free part of the body or peduncle which passes below into the coenosarc. This portion is retractile, and the zooid with its tentacles may be withdrawn for protection into the calycle.

The structure is that of Hydra. The outer layer is the ectoderm, the inner the endoderm, and the latter bounds a gastric cavity which extends throughout the stems and roots. The mesogloea which is developed between these layers is thin. The ectoderm of the zooid, especially that of the tentacles, is occupied by many stinging cells of a structure similar to those

of Hydra. The food obtained by the nutritive zooids is circulated in the general gastric cavity by the action of flagella developed by the cells of the endoderm.

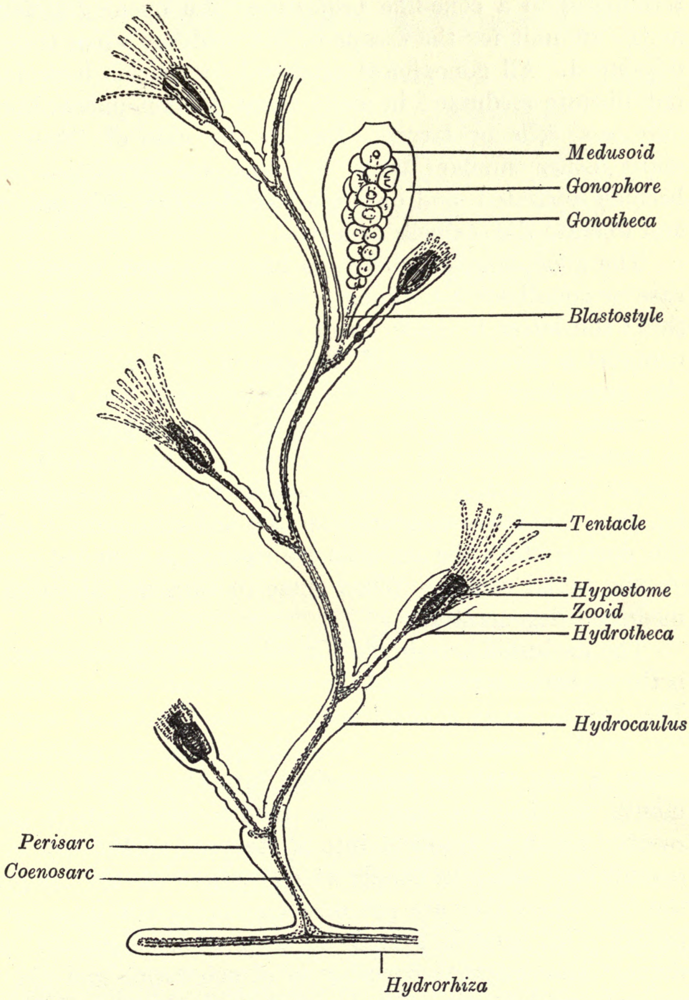


FIG. 17.—The hydroid stage of *Obelia geniculata.*

Reproduction takes place by the development of special outgrowths from the axillae of the branches of the stem. The outgrowth involves the ectoderm, the endoderm, and the

chitinous sheath. The reproductive zooid or gonophore when fully developed is enclosed, therefore, in a chitinous gonotheca; it is much larger than the hydrotheca, is elongated, and terminates in a cone-like projection. An opening is formed at the summit for the escape of the medusae when these are developed. All gonophores produced by marine hydroids do not liberate medusae: in many cases the gonophores liberate only sex cells or larvae. But in the case of Obelia and many other similar forms medusae are developed which become separated, and during a period of free existence ripen and liberate the sex cells or larvae.

The gonophore of Obelia, as has been seen, consists of a case or gonotheca containing a blind outgrowth of the coenosarc; the latter is made up of ectoderm and endoderm, and contains a diverticulum of the gastric cavity. This part of the gonophore is called the blastostyle. The blastostyle contracts, and at the same time bud-like outgrowths appear in succession along its walls. How these are gradually converted into medusoids will be plain from an inspection of fig. 18. The medusoids are liberated and commence a pelagic life, during which the sex cells are ripened in rounded clusters on the radial canals. When these in turn are liberated the medusoid degenerates.

The medusoid is umbrella-shaped; the outer convex surface is the umbrella surface, and the inner the sub-umbrella surface. The margin bears a large and variable number of tentacles, but usually twenty-four. From the roof of the sub-umbrella cavity a long stalk or manubrium projects, and it bears the mouth at the free end. The mouth leads into a gastric cavity, which is resolved into a stomach at the top of the manubrium, and four canals which radiate to the margin of the bell, where they are put into communication by a circular canal. This gastric system is lined throughout by endoderm. The external covering is of ectoderm, and the two layers merge at the mouth. Between the two layers the mesogloea forms a significant layer of a gelatinous nature. The margin of the umbrella presents a circular nerve associated with the ectoderm, and at intervals marginal sense organs, of which in Obelia there are eight at the bases

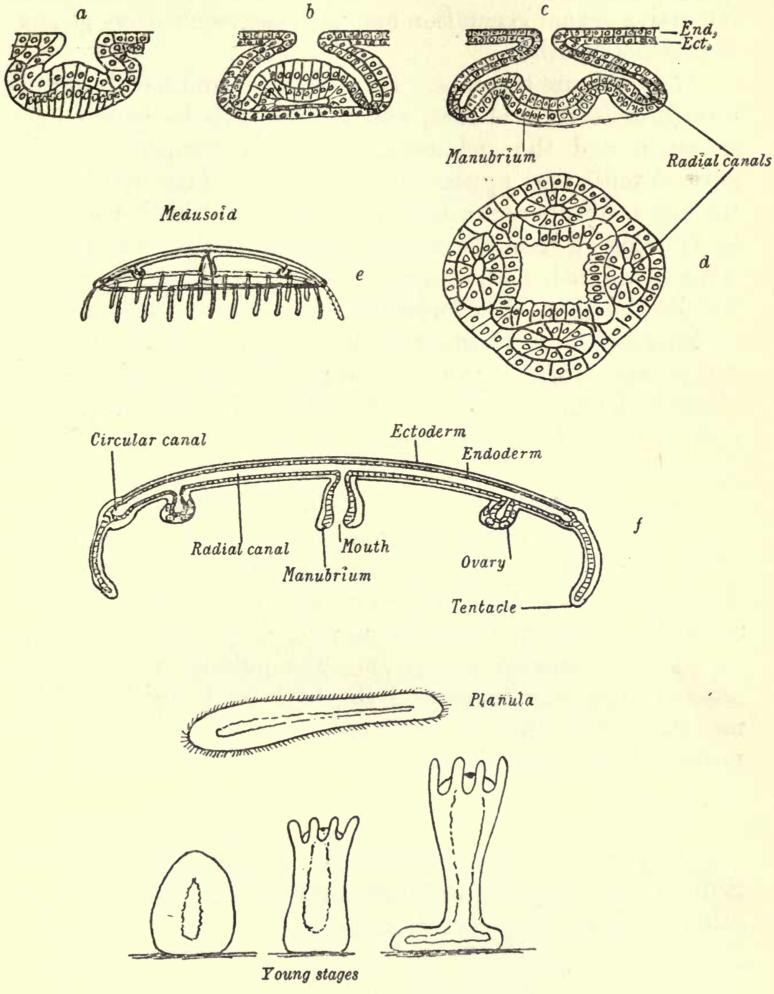


FIG. 18.—*Obelia geniculata.* Diagrams to illustrate (*a–c*) the development of the medusoid from the blastostyle, after Kühn. A plan (*d*) is also given of the developing medusoid viewed from the sub-umbrella surface, after Hadzi. The free medusoid (*e*) is shown and a vertical section (*f*) to indicate more exactly its structure. Larvae are developed in the female medusoid after the eggs are fertilised and they are called planulae. They are freed, and after a short period of freedom settle down and grow each into the hydroid.

of eight of the tentacles. The contrast in this respect between the active sexual generation and the passive nutritive generation is noteworthy.

The sexes are separate. Both the male and female gonads form prominent oval sacs, and the sex cells lie between the ectoderm and the endoderm. Sex cells cannot be distinguished until they appear in the medusa. After fertilisation the egg segments and a blastula is formed. This is converted by budding off from the interior into a planula. The planula larva is ciliated, and, escaping from the medusa, swims in a definite direction. The forward end is broad, and after a period of freedom the larva sinks to the bottom and the forward end is, after some exploration, applied to the weed or other object and broadens out to form a base of attachment. The posterior end of the planula, now the free end, develops tentacles and then a mouth, and by growth and branching the stolon and the stems of a new colony are established. Even before it is attached a cuticular secretion of the ectoderm forms, a prelude to the chitinous covering of the animal.

The medusa of Obelia is very small, measuring only a few millimetres, and in this state a wide dispersion takes place in tidal and aperiodic currents. The pulsations of the bell are sufficient only to control the horizontal position of the medusa, and to carry it across current to some extent. The medusa is altogether unable to swim against the currents of the sea.

During the spring this small medusa is very common in the shore region, and is procured in plankton nets along with many other beautiful medusae liberated by the species of other genera.

CHAPTER III

PLATYHELMIA

Phylum PLATYHELMIA		
Class TURBELLARIA		*Types*
TREMATODA	. . . . . .	Distoma
CESTODA	. . . .	Taenia
NEMERTINEA		

THIS phylum includes the Turbellaria, the members of which are often called Planarians and are distributed in fresh water, in the sea and on land, and are only rarely parasitic; the Trematoda and the Cestoda, which are parasites; and the Nemertinea, which are found mostly in the sea, but occur also in fresh water and on land, and are only rarely parasitic. The first three could be defined as aproctous Platyhelmia, for in them the intestine ends blindly; and the nemertines could be styled proctous Platyhelmia, as in their case the intestine forms an anal opening at the posterior end.

Distoma (Fasciola).—The liver fluke, *Distoma hepaticum*, of the sheep and other ruminants is usually easily obtained during the winter months from the liver of the sheep. It is of economic importance, producing the disease distomatosis, better known as liver disease or liver rot.

The adult worm is flat, and fluke or flat-fish like in shape, and is half to one inch in length. Large numbers may often be obtained from the bile tubes of the liver of the sheep, and the species has been recorded also from the ox, goat, camel, and wild ruminants, even from the horse, pig, and elephant, and it has been found in man. Another species, *D. lanceolatum*, has been found in the same or similar hosts. Both

are cosmopolitan in distribution, but *D. lanceolatum* is absent from the British Isles.

Distoma hepaticum has two suckers: one terminal and anterior and containing the mouth; the other, a short distance behind on the ventral surface, is large and projecting. The outer surface is smooth, but the cuticle, which is secreted

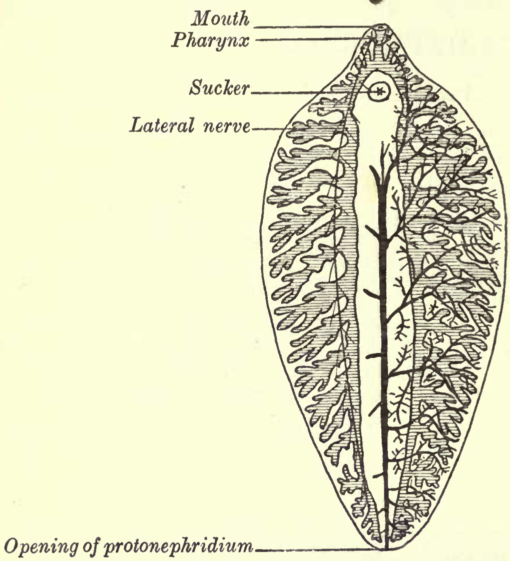


FIG. 19.—*Distoma hepaticum.* Somewhat diagrammatic ventral view to show the alimentary canal, the lateral nerve on the left, and the protonephridial excretory system on the right.

as a protective covering, is provided with numerous small sharp projections directed posteriorly. Much of the structure can be made out by examining the living worm in normal salt solution and by staining and mounting. The mouth leads into a short unpaired muscular pharynx, which opens into the intestine, and the latter immediately divides into two branches. These branches send out a large number of secondary branching tubes, all ending blindly near the margin of the body. The whole system is often seen clearly mapped out when distended by bile from the liver of the host. In *D. lanceolatum* there are no side branches to

the intestine. In *D. hepaticum* the branches of the intestine permeate all parts of the body, and the products of digestion are available at all points.

Another highly developed tubular system is that of the excretory organ. It begins in all parts of the body in hollow cells or solenocytes, each furnished with a tuft of cilia, the flickering action of which has suggested the name flame cell.

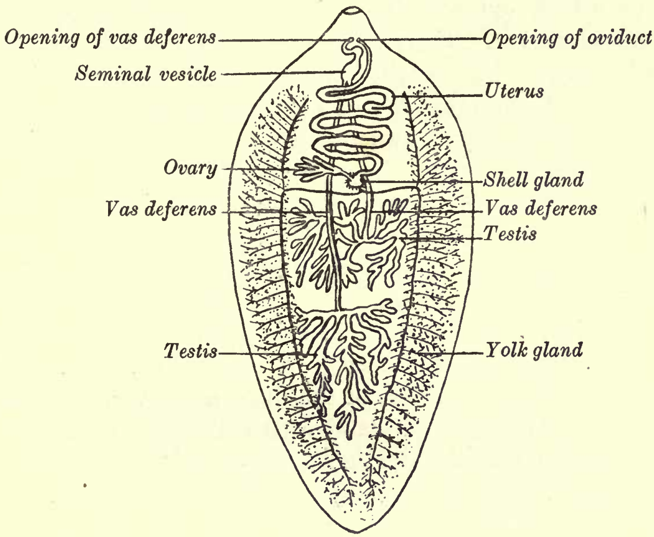


FIG. 20.—Similar view to the preceding to indicate the relationships of the various parts of the complicated reproductive system.

The branches gradually anastomose until they reach a duct which occupies the middle of the animal. This duct discharges through a pore at the posterior extremity. This kind of kidney is called a protonephridium, and is ectodermal in origin.

The nervous system is not very well developed, and it is difficult to make out. A nerve ring surrounds the pharynx. Two lateral ganglia are distinguished as swellings from which nerves pass forward to the mouth and the anterior sucker, and a pair of nerves which extend laterally to the hinder aspect of the body. Two dorsal and two ventral nerves

smaller than the lateral nerve pass backwards from the pharyngeal commissure.

The reproductive organs are highly developed and complicated. Trematodes are hermaphrodite. The openings of the male and female ducts to the exterior occur close together between the two suckers.

The male organs consist of two branched testes lying near the middle of the body. They each give off a vas deferens which extends forward to the neighbourhood of the ventral sucker. There they run into a median sac, the seminal vesicle. The seminal vesicle opens into the ejaculatory duct, the anterior end of which is invaginated to form a penis or cirrus, which can be withdrawn to form a cirrus sac or protruded beyond the male opening.

The female organs are made up of a dendritic ovary, from which issues the oviduct. Shortly after leaving the ovary the oviduct receives the vitellarian duct formed by the union of two ducts leading from the large yolk glands which lie along the sides of the worm. At this point also a short duct leads to the dorsal surface, where it opens by a pore. This is Laurer's canal. This part of the duct, moreover, is swollen and beset by the mass of gland cells called the shell gland. Beyond this region the oviduct becomes widened and convoluted, and ultimately ends near to the male opening.

The spermatozoa formed in the testes are passed along the vasa deferentia to the seminal vesicle and ejaculated by the cirrus into the Laurer's canal of another individual. The ova are fertilised, and during the time they are being surrounded by a horny shell by the shell gland they receive a quantum of yolk from the vitellarian duct. The eggs are then passed into the convoluted part of the oviduct, often called the uterus, and are shed through its opening into the bile duct of the host.

It is plain from the above and the figures, also by an inspection of specimens and preparations, that the fluke body, though thin, is occupied very fully by various ducts concerned with digestion, with excretion and reproduction. The organs are embedded in a mass of cells which extends from ectoderm to ectoderm, and these cells are more or less compact, forming

what has been called a parenchyma or mesenchyme. The spaces in the mesenchyme allow of a circulation of metabolic products. Some of the cells are converted into muscles, forming especially a transverse and a longitudinal layer close to the ectoderm, and the muscular coat of the pharynx.

Eggs are produced in great numbers, each individual providing, according to Thomas, some 4000. They undergo development in the egg case, but complete it only in favourable conditions—namely, in wet places, as pools and ditches. In such places the embryo escapes by the bursting of the lid or operculum of the egg case, after a free period of about one month. The larva, or miracidium, is ciliated. It is provided with a pair of adposed eye-spots, and in front with a papilla and internally with a pair of protonephridia. After being hatched the larva rarely lives a day if it does not meet its intermediate host, a common snail, *Limnaea truncatula*, found in ditches, ponds, marshes, and streams, and on land near these. It lodges in the pulmonary cavity of the snail, loses its cilia, and, becoming ovoid in shape, grows quickly into a sporocyst, the process lasting a fortnight in summer and a month in autumn. The sporocyst may divide and thus form daughter sporocysts. Cells are budded off from the inside of the wall of the sporocyst, and these cells by further division form masses which are converted into a number of rediae. The redia is also sac-like, but is provided with a mouth leading into a short alimentary canal. The rediae escape by rupture of the sporocyst and pass from the pulmonary cavity into the body of the snail and most frequently lodge in the liver. The redia grows to a size of about $1\frac{1}{2}$ mm. and gives rise to daughter rediae in summer, but in winter gives rise to cercaria. The cercaria is provided with two suckers, a forked intestine and a long tail. They make their way out of the snail, and, escaping into the water, swim about by the action of the tail and finally attach themselves to grass or water plants. When attached the tail is lost and a cyst of mucus secreted around the young fluke. The cyst hardens into a white envelope. It is now in the state when further development can only take place in the sheep. Eaten by the sheep the cysts are

removed by digestive processes in the stomach, and the young flukes make their way *via* the intestine to the liver,

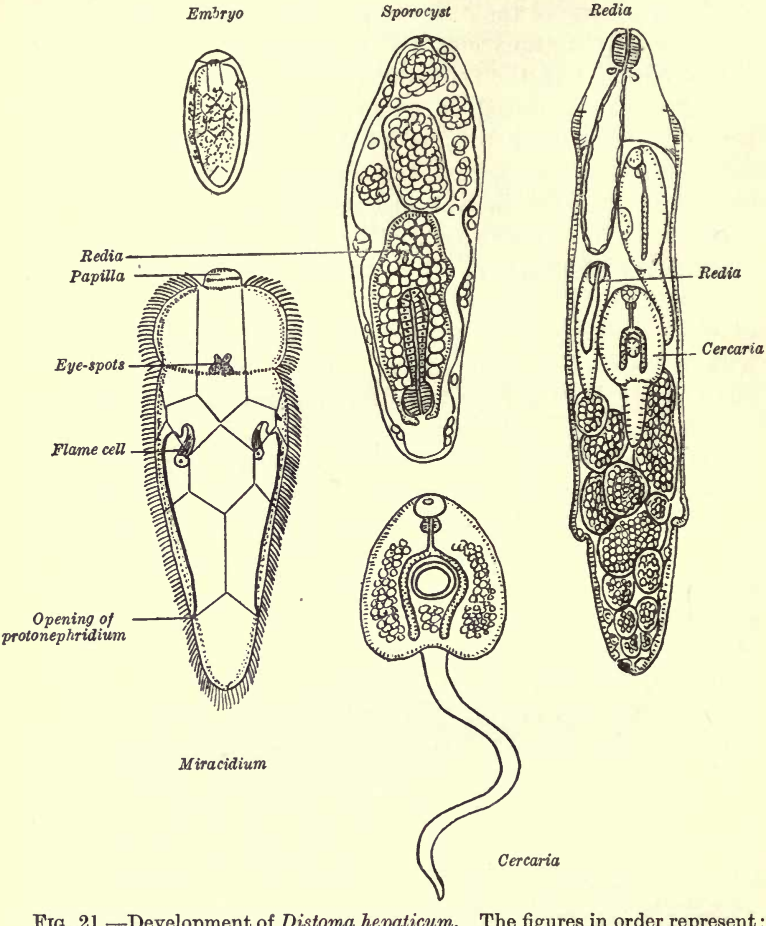


Fig. 21.—Development of *Distoma hepaticum*. The figures in order represent: the embryo in the egg case with remnants of the food yolk; the free larva, or miracidium (after Leuckart and after Coe); the sporocyst formed in the lung cavity of the snail, *Limnaea truncatula* (after Thomas)—the cells budded from the internal wall to form redia, one of which is shown; a redia from the liver of the snail (after Thomas), showing the formation of a daughter redia and of cercariae; cercaria, the tailed free stage (after Thomas), which becomes encysted on grass or water plants, losing its tail.

but whether by the portal vein or by the bile duct is not known. They usually remain in the bile ducts, but they have

been found also in the substance of the liver and are sometimes carried away in the blood stream to other parts of the sheep.

This account of the life-history goes to show why the disease is common in wet districts and in wet seasons. The descendants even from one ovum may amount to hundreds. It is in the autumn in temperate conditions that the sheep usually receive the infection of young flukes, and during the winter the sheep indicate by well-known symptoms, even by death, the effects. The eggs are discharged in large numbers and are found in the faeces of the sheep. Draining wet land has been proved to be an effectual method of prevention, and, following the observation that salt marshes are immune, applications of salt have been found to be beneficial. It is obvious also that good will result from regulating the movements of sheep so as to prevent the eggs from developing, and the sheep from infection.

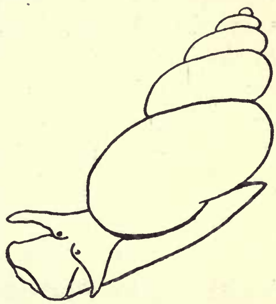


FIG. 22.—*Limnaea truncatula.* The shell measures only 6–10 mm. in height.

It is interesting to note that the life-history was worked out independently by Leuckart in Germany and by Thomas in England.[1]

Taenia. — Cestodes, or tapeworms, are parasitic in vertebrates in their adult state, and the young phase is also parasitic and is passed usually also in a vertebrate, sometimes in an invertebrate, host. The final host gets its infection by eating the intermediate host, and the latter is infected by swallowing the eggs, or, in the case of aquatic animals, from the larvae liberated by the eggs.

Some tapeworms are of economic importance. Thus *Taenia solium* of man is obtained from measly pork. *Coenurus cerebralis*, which is found in the dog, causes during its young stage a disease in sheep called 'sturdy.' In this case the intermediate stage is a coenurus characterised by the development of a bladder possessing many heads or scoleces

[1] 1881–82, Leuckart, *Zool. Anz.*; 1882–83, Thomas, *Jour. Agri. Soc.*

in or about the brain of the sheep. An allied form passes between the rabbit and the dog. In the rabbit the coenurus is lodged usually near the armpit.

The tapeworm chosen for special study is *Taenia serrata*, which occurs in the adult condition in the dog and is derived from the *Cysticercus pisiformis* so common in the peritoneal cavity of wild and domestic rabbits.

The adult tapeworm is fastened to the wall of the intestine of the dog by the head or scolex. The scolex is provided with a ring of about thirty-six hooks, alternately large and small, situated on a prominence called the rostellum, below which are four suckers, all about equally distant from one another in a transverse row. This region is succeeded by a short unsegmented neck, only slightly narrower than the scolex. The rest of the body is about a yard in length and is segmented, each segment being called a proglottis. The proglottides are flat expansions of the body and gradually increase in width. At first—that is, near the neck—the segments are short, at a distance of about a foot from the scolex they are almost as broad as long, and the length gradually increases in the following segments. With increase in length the proglottides present lateral projections which bear the genital pore in each case (fig. 23).

The structure of this tapeworm as a whole is simple. The ectoderm forms an external covering and the cells project below into the muscle layer ; it secretes a cuticle externally. Below the ectoderm there are longitudinal muscles and circular muscles, and the rest of the space internally is occupied by a mesenchyme in which certain other organs are embedded. There is no mouth nor alimentary canal. Two longitudinal nerves, one on each side of the worm, run from end to end and merge in the scolex in a ring. The excretory system consists of longitudinal canals which receive branches all along their length, branches which begin in flame cells or solenocytes. It is a protonephridial system, and it opens terminally on the last segment by a single pore which is renewed as the segments are cast off. The food is imbibed through the cuticle which protects the worm from the digestive juices of the host ; it is already digested and is circulated in the

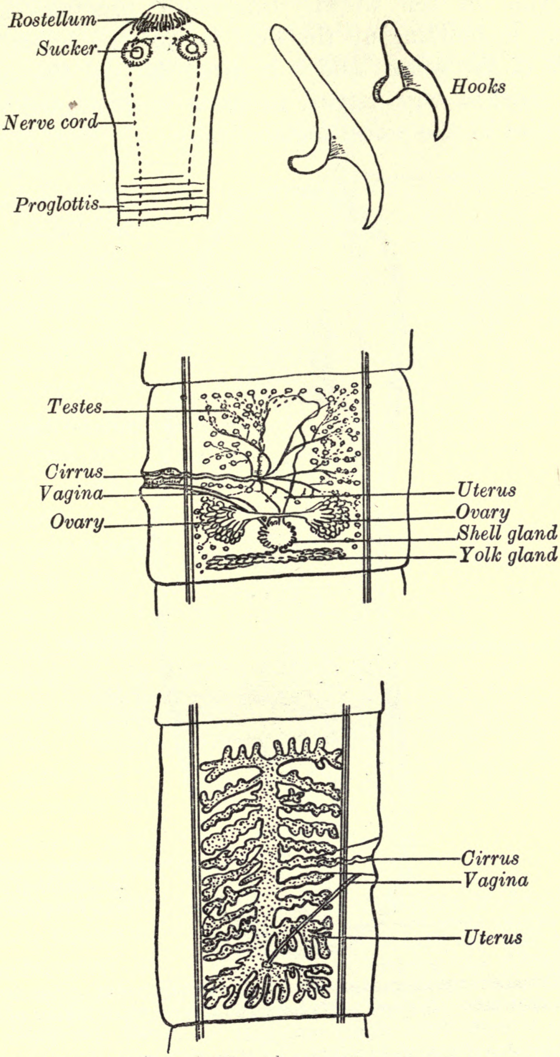


FIG. 23.—*Taenia serrata.* The figures in succession show the head, or scolex, with suckers and hooks. Enlarged views of the two kinds of hooks are given at the side. The middle figure is of a proglottis constructed from several proglottides of the anterior of the worm, showing the relationship of the generative apparatus. The lower figure is a terminal segment showing the expanded condition of the part of the oviduct termed the uterus, which contains a large number of eggs.

parenchyma of the worm. Enzymotic processes are only necessary in building up the food to suit the constitution of the cells of the worm, and it is probable that the specificity usually marked with regard to hosts is connected with the peculiarities of the worm metabolically.

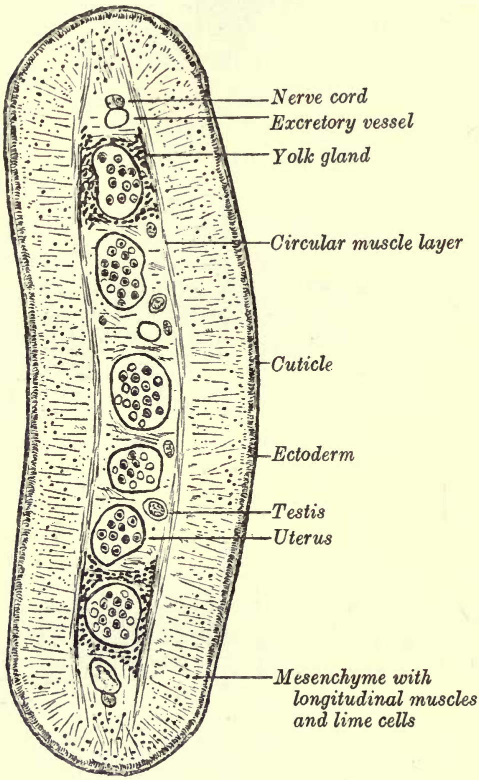


Fig. 24.—Transverse section of another common tapeworm of the dog, *Dipylidium caninum*. *Note*—In this form the reproductive organs are paired.

The proglottides are concerned in forming the generative organs. The latter are initiated just behind the neck and pass through phases of development in the successive segments, culminating in the terminal segments, which are full of eggs. The proglottides are being constantly renewed in the neck, and the ripe segments are cast off from the posterior end.

Each segment is hermaphrodite. Clumps of cells appear first which are testes, and ducts arise in association with them. These are vasa deferentia and culminate in a single coiled vas deferens. This opens to the exterior on the side of the segment on the projection containing the genital pore. Terminally the duct is eversible in the form of a penis or cirrus. Two ovaries are developed, the ducts of which meet and fuse. Just after fusion the oviducts receive the vitellarian duct from the yolk glands, and at the same place it is surrounded by the shell gland. Here also it gives off a diverticulum for the storage of the eggs, and this is called the uterus. The duct then passes to the genital pore, or atrium, where it opens close to the opening of the vas deferens. There is reason for believing that this last part of the duct corresponds to Laurer's canal of the Trematodes, and that the uterus is the original oviduct which has lost its external opening. The sperms are

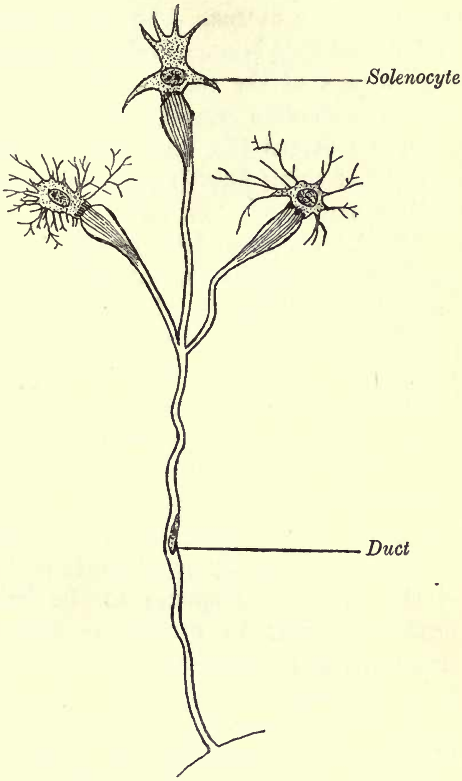


FIG. 25.—Three solenocytes of the protonephridium of *Taenia crassicolis* of the cat, after Bugge and Meisenheimer. The solenocytes have each a nucleus, the cytoplasm sends amoeboid processes into the mesenchyme spaces, and each of the cells is formed into a long tube which bears above a tuft of cilia and is continued below to form the beginning of the excretory duct. The fourth nucleus is that of the cell forming the collecting duct.

introduced, it is believed, by cross-fertilisation when possible into the oviduct, which thus acts as a vagina and spermatheca. The eggs are fertilised, and together with a quantity of yolk are covered by a shell. The eggs as they are completed are passed into the uterus. The uterus thus becomes greatly distended, and as it becomes filled with eggs it gradually occupies a great part of the space available in the segment, and the other reproductive organs become correspondingly reduced.

In the uterus the eggs undergo their early development, an embryo being formed provided with six hooks and called the hexacanth.

The detached proglottides passed out from the dog in the faeces are scattered about on pastures, and, if the intermediate hosts do not become infected with them immediately, the proglottides gradually decay and the eggs are liable to further dispersion. When the eggs are eaten the coat surrounding them is digested in the stomach of the rabbit and the hexacanth liberated. The hexacanths obtain entrance to the blood by burrowing through the wall of the stomach or intestine and are conveyed by the portal circulation to the liver. Their presence in the liver is marked as early as the second day by small white nodules formed in the liver of the rabbit in response to the irritation produced. The further progress in growth is traceable by haemorrhagic streaks, which become sinuous and increase in size, either in or on the surface of the liver. These contain the cysticerci more or less surrounded by coagulated blood. The interlobular blood-vessels containing the cysticerci become obliterated, and the cysticerci are enclosed in a sheath formed around them by the leucocytes of the blood. The cysticercus at this stage is an elongated vermiform body. It consists of a thick-walled sac invaginated at one end, and the cup has projecting into it a scolex. It is probable that it multiplies by transverse fission. In about a month the cysticercus is in a condition to quit the liver. It enters the peritoneal cavity and again becomes encysted, singly, or in clusters, around the stomach or in other parts of the peritoneal cavity. It cannot undergo further development unless it is eaten by the dog.

When it is introduced into the stomach of the dog the cyst is dissolved and the young tapeworm fastens itself to the intestine, and the bladder part being discarded, it proceeds to grow into a tapeworm.

The area of attachment of the tapeworm to the intestine is tumified and the cells altered. The tapeworm, besides

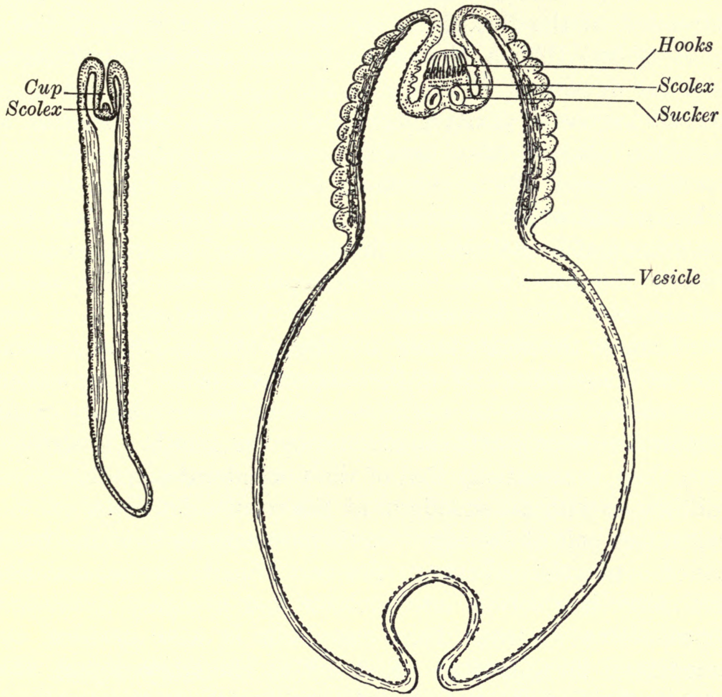


FIG. 26.—Cysticercus of *Taenia serrata* from its gallery in the liver of the rabbit, and the more mature cysticercus (*C. pisiformis*) from its cyst in the peritoneal cavity of the rabbit.

imbibing the food of the host, liberates secretions which have a poisonous effect, and when they are present in large numbers the effects may be serious. In the cysticercus or the corresponding stage, the effects on the intermediate host may be very great, especially in the case of compound larvae, as Coenurus in the brain of the sheep, and Echinococcus larvae,

which form hydatid tumours in the liver of the sheep and other animals.

General Considerations.—The parasitic Platyhelminths have undergone great modification and degeneration in adapting themselves to their strange life-histories. Their structure, therefore, is more interesting from the point of view of the effects of parasitism than from the morphological. A consideration of the free allies, the Turbellaria and the Nemerteans, shows that a blastula is formed and that endoderm cells are developed at one pole, the vegetable pole, and may indeed enclose a cavity communicating with the exterior, a primitive enteron being produced, and the opening is termed the blastopore. From the same region also a mass of cells is budded off which intervenes between the endoderm and the ectoderm and is resolved into the muscles and the mesenchyme. This is the mesoderm. The blastopore, or the region which corresponds to it, is carried inwards by the growth of the ectoderm as the stomodeum, and forms the mouth and some part of the anterior end of the alimentary canal. But, as has been stated, unless in the Nemertinea, the alimentary canal communicates only with the exterior by the mouth. The structure, then, is essentially that of the Coelenterates, an ectoderm continuous with an endoderm at the mouth developed at the vegetative pole of the egg. To these structures there has been added a mesoderm between the two primary layers, and the mesoderm is resolved into muscles and a highly developed reproductive system. This mesoderm is also invaded by ectodermal invaginations which act as excretory organs, the protonephridia. In the case of the Nemertinea the mouth is also developed from the blastopore, but the posterior end of the intestine establishes an anal opening later.

The primary layers of the Metazoon are the ectoderm and the endoderm, and the Platyhelmia have interposed between them a third layer, or mesoderm, which gives rise to organs connected with reproduction, to muscles and to spaces in which metabolic products circulate. The spaces represent a primitive body cavity and may, as in the wheel animalcules (Rotifera), and the larvae presently to be described, be so

expanded as to form a single cavity—a cavity containing a watery fluid, across which the ectoderm and the endoderm are connected only by thin threads of the original mesoderm. The space, like the mesenchyme of the flat worms, is invaded by protonephridia derived by invagination of the ectoderm, and they end blindly in flame cells or, as they are now generally termed, solenocytes. This primitive body cavity is called the primary body cavity, or schizocoel, and the cells which occur within it are derived from both ectoderm and endoderm.

A secondary body cavity, or coelom, is developed in the remaining groups of animals typically, and they may be thus described as Coelomata. It is derived from the endoderm, and the cells form a cavity distinct from the schizocoel. An anterior schizocoel and a posterior coelom are thus present in the early Coelomata. The appearance of a coelom is correlated with the formation of blood and vessels by the cells of the schizocoel, which thus preserve their primitive function of circulating the metabolic products. It is obvious that an expansion of the coelom can take place only at the expense of the schizocoel, and *vice versa*. The coelom in some undoubted Coelomata may be suppressed.

The coelom is, however, not a new formation. In the Platyhelmia the mesoderm is resolved into a tubular system, concerned with the development and the discharge of the sex cells, and a primary body cavity. The Platyhelmia, like the Rotifera, have, in other words, a gonocoel and a schizocoel. The gonocoel in the Rotifera is derived from the endoderm, and may, indeed, be said to have this origin in the Platyhelmia. The coelom is the expanded gonocoel, and, invading the territory of the schizocoel, it takes over to some extent the excretory function. The protonephridia either establish an opening into the coelom, or are suppressed and special ducts developed from the coelom which are called coelomiducts.

A coelom emerges in a group of animals which are all so intimately connected at their roots, although divergent in their stems and branches, that it is difficult to separate them

satisfactorily.[1] In the following arrangement the Rotifera are acoelomate, the rest are coelomate :

Phylum TROCHOZOA

Sub-Phylum	ROTIFERA . .	Wheel animalcules
	MOLLUSCA . .	Shell fish
	NEMATOMORPHA .	Horse-hair worm
	PODECTATHENTA .	Sea mats, lamp shells, etc.
	NEMATODA . .	Threadworms
	ARTICULATA .	Insects, Crustacea, etc.

[1] 1909. Rauther, *Morphol. und Verwandtschaftsbez. der Nematoden* ; *Ergeb. u. Fortschr. d. Zool.*, Bd. I.

CHAPTER IV

MOLLUSCA

Phylum TROCHOZOA
Sub-Phylum MOLLUSCA

Class AMPHINEURA	*Type*
GASTEROPODA	
SCAPHOPODA	
PELECYPODA . . .	Anodonta
CEPHALOPODA	

THE Mollusca include the eight-shelled chitons and their allies (Amphineura); the univalves, or snails, slugs, buckies, etc. (Gasteropoda); the tooth shells (Scaphopoda); the bivalves, as oysters, clams, mussels (Pelecypoda); and octopuses, squids, and cuttle-fish (Cephalopoda).

Although bivalve Mollusca are common in the sea, there are many species which are found only in fresh water. These have been grouped under several allied families, of which the Unionidae is important from the economic value of species of Unio. This family is world-wide in distribution, but predominates in the south.

Anodonta.—The fresh-water mussel, *Anodonta cygnea*, is common in rivers and in ponds of the northern hemisphere, and is spread over Europe, Asia, and North America. The genus is found also in South America. It is so closely similar in structure to other members of the Unionidae that the following description will enable the dissection of any species to be readily followed. There is little essential difference between it and the large siphonate species so common on mud flats and in shallow bays in the sea, as the clam, *Mya arenaria*, and the gaper, *Lutraria elliptica*.

The fresh-water mussel inhabits the mud, the anterior end being buried and the posterior end exposed. The foot enables it to progress slowly by ploughing through the mud. The food is suspended matter, detritus, and minute organisms.

External Morphology.—Each valve has a rounded anterior border and a pointed posterior border. The lines of growth follow the contour of the shell and indicate the history of the shell. They centre dorsally in a small rounded projection which is the nucleus of growth of the shell, and it is occupied also by the larval shell or by a scar which marks the position

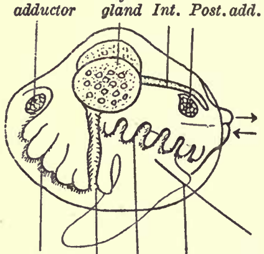


Fig. 27. — Larva of *Mya arenaria* with velum retracted and foot protruded.

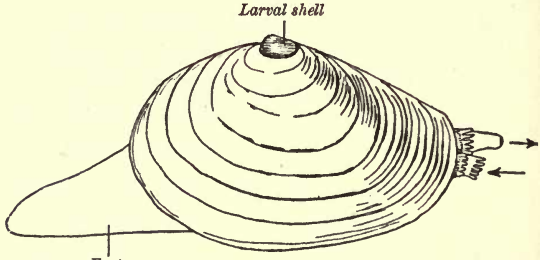


Fig. 28.—Young *Mya arenaria,* to show position of the larval shell (that of fig. 27) on the umbo of the adult shell. After Jackson.

of the larval shell. This prominence is styled the umbo. The two valves are hinged by a straight edge, the dorsal hinge line, and are connected by a ligament, which extends from a point a little in front of the umbo to the end of the hinge line behind it. The ligament is elastic and tends to open the valves, and in the living condition it is compressed by the adductor muscles.

Internally the shell has a pearly appearance and is smooth. The general internal aspect is similar to that of the external surface, and the hinge line and the ligament have already been seen. Along with lines which express the growth of the shell certain impressions will be observed which indicate the history and the attachment of muscles. These will be identified as anterior adductor, anterior retractor, anterior

protractor, posterior adductor, and posterior retractor, the present position of each being marked by the broad terminations of triangular-shaped areas which indicate the migration and growth of the muscles. The adductors close the shell, the others are related to protruding or withdrawing the fleshy foot and are paired. The attachment of the mantle fold, which in life lies close to each valve, may be traced in a line near the ventral border of the shell, which it follows from the ventral aspect of the anterior adductor to that of the posterior adductor. This is the pallial line, and in species in which the posterior openings are carried out on a siphon it is indented posteriorly, forming the so-called pallial bay. The bay is associated with the provision for the retraction of the siphon.

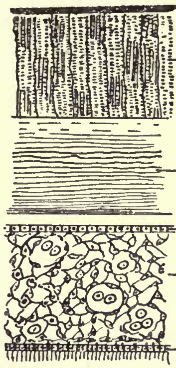


FIG. 29.—*Anodonta cygnea.* Section of shell and mantle.

A section of the shell shows that it consists of three layers, the outer chitinous layer, periostracum, which is uncalcified, a prismatic layer—both of these are formed at the margin of the mantle—and a nacreous or pearly layer which is secreted by the mantle as a whole. It is to be observed that the shell is altogether outside the body and is secreted by the action of the external ectoderm of the mantle and the continuation of the external ectoderm over the dorsal part of the body.

The mantle which produces the nacreous layer of the shell forms pearls in various Mollusca, notably in certain Pelecypoda. The pearl is initiated by an irritant, and usually in nature by a larval trematode or cestode. The parasite comes to lie between the mantle and the shell, and the outer ectodermal layer of the former begins to secrete layers of nacre around it, but the process is a slow one. According to the position of the parasite, the resulting pearl will be free or more or less attached to the shell. A perfect or fine pearl is formed in an ectodermal pocket of the mantle. Lyster

Jameson has demonstrated the part played by *Distoma margaritarum* in the formation of pearls of the common bait mussel, *Mytilus edulis,* and Boutan emphasised the fact that the pearl is always produced in a pouch formed by the outer mantle epithelium. It is believed that oriental pearls are provoked by a Distoma, perhaps the same as that of the common mussel, or one closely allied to it. Birds are the final hosts of this parasite, and the mussel is probably the second of two invertebrate hosts. Herdman and Hornell found that the pearls of Ceylon resulted from a cestode parasite in the larval state, and probably other larvae may be found to be encysted in mussels with pearl formation. Methods of culture have been extended to the encouragement and protection of pearl fisheries in the East Indian region, and with notable success in Japan. Encouraging success has followed also the artificial stimulation of the mantle in the formation of blister pearls or half pearls by trepanning the shell and introducing artificial nuclei. Perfect pearls have been produced artificially in Japan, and they are apparently little different from the costly fine pearls of the Eastern fisheries.[1]

The bilateral symmetry expressed by the valves of the shell is likewise characteristic of the animal protected by them. The mantle lobes, which depend sub-equally on each side, are lateral expansions of the dorsal region of the body. The outer ectodermal layer which is applied to the inner face of the shell is firmly attached thereto along the pallial line. Beyond this, it ends in a ventral border extending from the region of the anterior to the posterior adductor muscles. The inner epithelium of the mantle is ciliated and is continuous with the ciliated ectodermal layer of the gills and foot. The two folds of the mantle fuse posteriorly and divide the opening into a ventral inhalent and a dorsal exhalent opening. The mantle is thickened in the region of the respective openings. The margin of the lower opening is produced into tentacular processes, and it is limited at its ventral angle by the approximation of the borders of the mantle. The visceral mass of the mussel is situated dorsally and medianly, and

[1] 1902, Jameson, *Proc. Zool. Soc.*; 1903, Herdman, *The Pearl Fisheries of Ceylon*; 1904, Boutan, *Arch. de Zool. expér. et génér.*, 4me Sér., T. 2.

protruding from it ventrally are the median foot, and laterally the two pairs of gills and the folds around the mouth known as labial palps. The space bounded by the mantle folds and containing these organs is the mantle or pallial cavity. The gills are large expansions of the body wall on each side and are developed as filters of the water introduced into the mantle cavity through the inhalent opening. They are disposed in flattened outer and inner pairs, and each consists of an outer and an inner lamella enclosing a cavity. Each lamella is pierced by vertical and horizontal slits dividing the lamella into filaments, and these put the mantle cavity in communication with the inner cavity of the gills. The gill filaments are strengthened by chitinous rods and are connected by interfilamentar junctions at intervals, and the lamellae are similarly connected by interlamellar junctions. The outer lamella of the external pair of gills is continuous with the inner face of the mantle, the inner lamella with the outer lamella of the internal gill. The inner lamella of the latter is attached anteriorly to the ectoderm of the visceral mass. It ends freely, however, on either side of the foot, and behind the foot the inner lamellae of the two inner gills fuse, and by further fusion the cavities of the gills are reduced to a single cavity which discharges through the exhalent opening, a cavity which, since it receives besides the excretory products from the kidneys and the egesta from the alimentary canal, has been called a cloaca.

Internal Morphology. **Alimentary Canal.**—The mouth lies medianly between the anterior adductor muscle and the foot, and it is fringed with lips which are drawn out on each side into ciliated sensory processes, the labial palps. These take up the food gathered by the mantle cavity. The mouth leads upwards by a short oesophagus to the stomach, a wider part of the tube with folded walls which receives the openings of the digestive gland. The tubules of the gland form a dark mass around the stomach, and the organ is usually known as the liver. The intestine leaves the stomach on the ventral side and passes into the foot, and after a course in the foot, indicated in fig. 30, it is directed dorsally and then horizontally to pass through the pericardial cavity. In this cavity

it serves as a support for the heart. The intestine opens posteriorly behind the posterior adductor. The ascending loop in the visceral mass and the remaining posterior part of the intestine is provided with a ridge, the typhlosole, on its ventral surface, and the straight part of the intestine is called the rectum. The whole canal is richly ciliated.

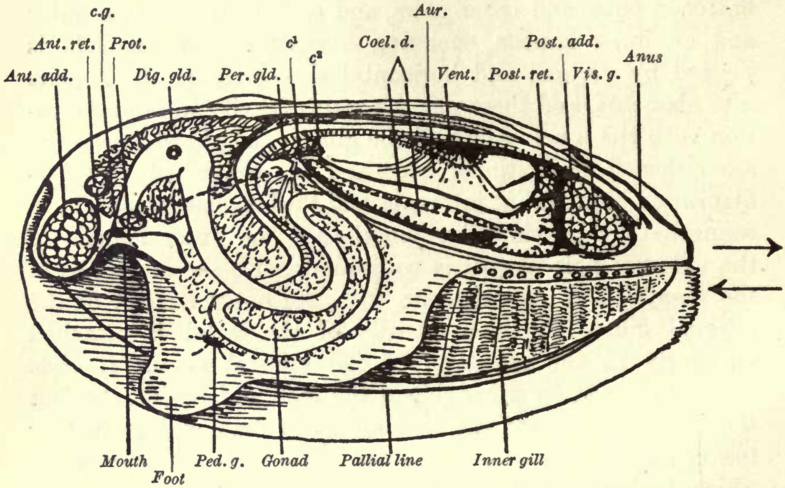


FIG. 30.—Anodonta. General dissection from the left side. The nerve commissures are indicated by dotted lines. *c.g.* = cerebral ganglion. *Vis. g.* = visceral ganglion. *Ped. g.* = pedal ganglion. c^1 = outer and c^2 = inner opening of coelomiduct (*Coel. d.*). *Per. gld.* = pericardial gland.

The intestine may be found to contain a peculiar glassy rod, the crystalline style. In the clam, and commonly in Pelecypoda, it occupies a special caecal diverticulum of the stomach. It is produced as a mucous secretion, and becomes rod-like by the action of the cilia. It is believed by some to be a reserve of food for winter, by others to act as an aid to digestion by providing a reserve of enzymes, and it may have a use in preventing rough particles of food from damaging the tender epithelial wall of the intestine. The rod contains proteid material and enzymes.[1]

[1] 1918. Nelson, *Jour. of Morph.* vol. 31.

The greater part of the alimentary canal is embedded in other organic systems, and it is distinctly seen only as it passes through the pericardial cavity.

Coelom.—The pericardial cavity is the main part of the coelom or body cavity, and is restricted to a region of the body dorsally in front of the posterior adductor. The intestine

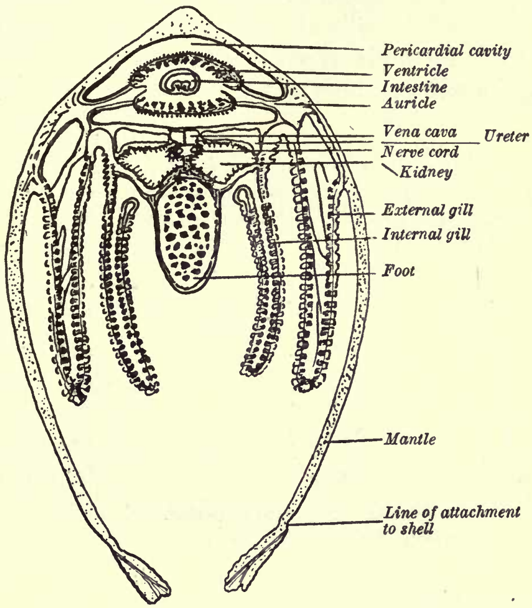


FIG. 31.—Anodonta. Transverse section in region of heart. The shell is removed.

and the heart may be easily seen through the thin wall. In front it receives the openings of Keber's gland or the pericardial gland, which is excretory and spreads on each side of the front of the pericardial cavity. It communicates with the exhalent system by a pair of coelomiducts or kidneys, the organ of Bojanus. The internal openings of the coelomiducts are situated at the extreme anterior end of the cavity, and the external openings on each side opposite to them on the body wall in the cavity of the inner gill. If the gill cavity be opened in this region two small apertures will be disclosed, just at the place where the dark part of the kidneys ends

anteriorly. The upper of these openings is that of the coelomiduct, and the lower is that of the gonad.

Between the two openings the coelomiduct is disposed in a loop. From the inner opening the duct passes posteriorly to the posterior adductor and is dark in colour, the epithelium being glandular and thrown into folds. This tube removes the excretory material from the blood. At its posterior end it gives off dorsally the thin-walled portion of the tube, which extends forwards over the glandular portion to open as stated by the external aperture. This thin-walled part of the coelomiduct is thus interposed between the glandular part and the floor of the pericardial cavity, and is frequently termed the ureter. The ureters meet and fuse anteriorly just before they diverge to reach the external openings. It is important to note that the pericardial cavity is a closed one and communicates with the exterior only by the coelomiduct. The gonad, which is tubular, is also a derivative of the coelom.

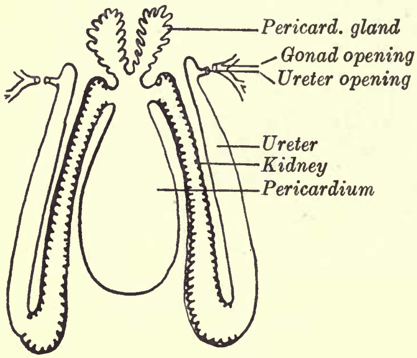


Fig. 32.—Anodonta. Diagram of pericardial cavity and coelomiduct.

Vascular System.—The blood is colourless, consisting of a plasma slightly tinged with haemocyanin, a respiratory pigment associated with copper, and the blood cells are leucocytes. It circulates in vessels and irregular spaces or lacunae interposed between the ectoderm and the organs. The heart is primitively dorsal in position. The ventricle, however, is enclosed in a fold of the pericardial cavity, and it is besides wrapped round the rectum, which thus appears to pierce it. Arterial blood is conveyed to the ventricle from the gills by a pair of delicate auricles. The auricles are broad at their lateral borders where they originate from the lateral wall of the pericardial cavity, and they narrow as

they cross the pericardial cavity to reach the median ventricle, into which they open, each by an aperture guarded by a pair of valves. The ventricle by its pulsations propels the blood into anterior and posterior aortae. The inner layer of the pericardial cavity is involved in the contractions of the ventricle and its cells are modified. The anterior aorta lies along the dorsal aspect of the rectum and divides into arteries

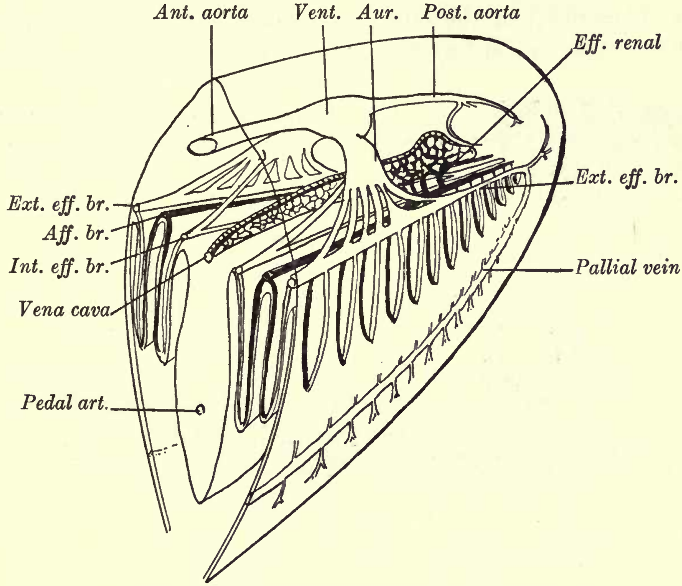


FIG. 33.—Anodonta. Diagram of circulatory system.

supplying the foot, digestive glands, stomach, and intestine, as well as all the anterior part of the body. The posterior aorta passes posteriorly from the ventricle on the under side of the rectum and supplies that part of the intestine and the neighbouring parts of the body. Both the aortae supply blood to the mantle. In all parts of the body and mantle the arteries split up into small arteries, and these are lost in spaces or sinuses from which the blood is collected into veins. The veins run into larger veins and ultimately, in the case of the mantle, into the large paired pallial veins, and that of the body generally into the paired, adposed venae cavae. Each

of the former runs round the mantle and returns the blood to the external efferent branchial trunk both anteriorly and posteriorly; the blood is arterialised, for it has been in contact with the water of the mantle cavity. The venae cavae lie under the pericardial cavity and send the blood to sinuses surrounding the glandular part of the kidney. Efferent renal vessels carry the blood from the kidney to the gills. The collecting vessel or afferent branchial trunk runs along the attachment of the outer and inner gills on each side, and the blood is carried by afferent branchial veins into the sinuses of the gills. In the gills the blood passes through spaces containing lymphoid tissue and through the blood spaces of the filaments. The blood is returned from the gills by efferent branchial veins which culminate in the efferent branchial trunks — internal and external. The external trunk receives veins from the pericardial gland on each side. The efferent branchial veins are joined, as has been said, by the pallial veins anteriorly and posteriorly, and the combined arterial blood is then sent into the auricle on each side of the body, which also receives the blood from the internal efferent branchial trunk.

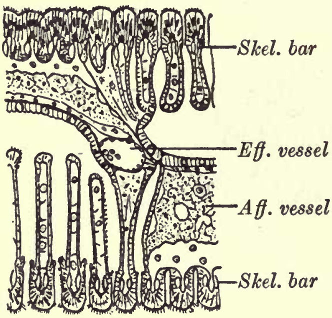


FIG. 34. — Anodonta. Transverse section of external gill, showing an intralamellar junction.

Nervous System.—The nerve ganglia in the fresh state are of an orange colour, and the nerves associated with them are white and fine. The cerebral ganglia may be seen without dissection just above the mouth and between the anterior adductor and the protractor muscles. The pair of pedal ganglia are situated close together medianly in the foot, just above the muscular part of the foot. They may be exposed by splitting the foot longitudinally or by dissection, following the course of the cerebro-pedal commissure. The pair of visceral ganglia lie close together on the under side of the posterior adductor. The cerebral ganglia are connected by

a commissure which lies anteriorly to the oesophagus. They supply the palps and neighbouring parts, including the anterior muscles. Each ganglion is connected also to the pedal and the visceral ganglia by commissures. The former is easily followed, for it runs straight from the one ganglion to the other. It is accompanied by a nerve supplying the otocyst or balancing organ, a pair of which occur just behind the conjoined pedal ganglia. The connective between the cerebral and the visceral ganglia runs upwards and backwards after leaving the cerebral ganglion, and then pursues a straight course to the visceral ganglion. It comes prominently into view as it passes on the inner side of the dark kidney.

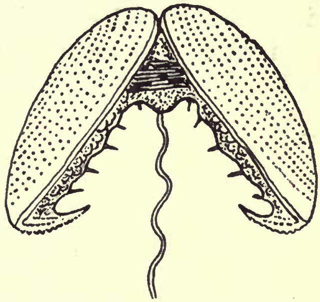


FIG. 35.—Anodonta. Glochidium larva from external gill. The attaching thread, which is indicated only in its proximal portion, depends medianly.

Reproductive Organs. — The sexes are separate. The ovaries, as also the testes, occupy the visceral part of the foot. The alveoli fuse to form ducts which merge in a common duct on each side, the external opening of which lies in the cavity of the inner gill below the opening of the coelomiduct. The spermatozoa are carried out of the mussel by the exhalent current and gain entrance to the females by the inhalent currents. The eggs are passed into the chamber of the outer gill, where they are fertilised and develop into larvae, styled glochidia, and the gill, during the season of reproduction, is distended by their presence. The glochidia are provided with bivalve armed shells, an adductor muscle, and the small foot secretes a sensitive, adhesive thread. The glochidia are discharged when fish are near, and attach themselves to the body or the fins. The thread contracts and the glochidia become attached firmly to the skin, a tumour or cyst resulting in which the development is completed. When the adult features of structure have been acquired, the young mussel leaves the fish and falls to the bottom to begin its adult life.

General Considerations.—Structurally and physiologically

the bivalve Mollusca are remarkably consistent. The mouth is anterior, but the food is introduced into the body by an opening at the posterior end. This opening may be removed still further away by the inhalent opening being carried out on a siphon, e.g. Mya, Lutraria. In some cases, as Scrobicularia and Teredo, the inhalent tube and the exhalent tube are independent and are capable of active movements, and may be retracted and protracted. The food, which is nearly always suspended material, is carried by ciliary action with a large volume of water into the mantle or pallial cavity. The water is filtered by the gills, and the food matter, entrapped in mucus, is carried by ciliary action to the region of the labial palps, and so to the mouth. The gills therefore are not merely branchial in function, and it has been suggested that their blood may take up dissolved food as well as oxygen from the water. It is obvious that the success of the bivalve depends upon the supply of food in its neighbourhood, for the mussel has only a limited range, and besides it is necessarily gregarious.

The adductor muscles close the shell by active contraction of the fibres, and in the case of bivalves exposed to the air the shells have to be kept tightly closed for a long time, and in that of oysters and mussels packed for market for many weeks. It would obviously be a severe physiological effort to maintain the contraction by a constant succession of stimuli, and it has been found that the contracted fibres are locked automatically in the contracted state, and can only be released when a stimulation reaches the locking fibres.

Bivalves lead as a rule a sedentary life, and are so protected by the valves as to be only subconsciously interested in their surroundings. Some, as Pecten, are active, and in association with the activity develop additional sense organs. They are subject during the course of their years of life to a summer increase in growth, in physiological activity and reproduction, and to a state of relative rest in the lower temperature conditions of winter, and such alternations are recorded in the growth of the shell.

In the young state Anodonta and its allies are liable to considerable spread when parasitic on fish. In North America,

where the Unionidae are very common, all classes of fresh-water fish are used by the members of the family, including the ganoids.

In the sea the Pelecypoda are spread as larvae, which are subject to drift in tidal and ocean currents. The larva is known as a trochophore, and its development and structure are interesting and important. During segmentation changes

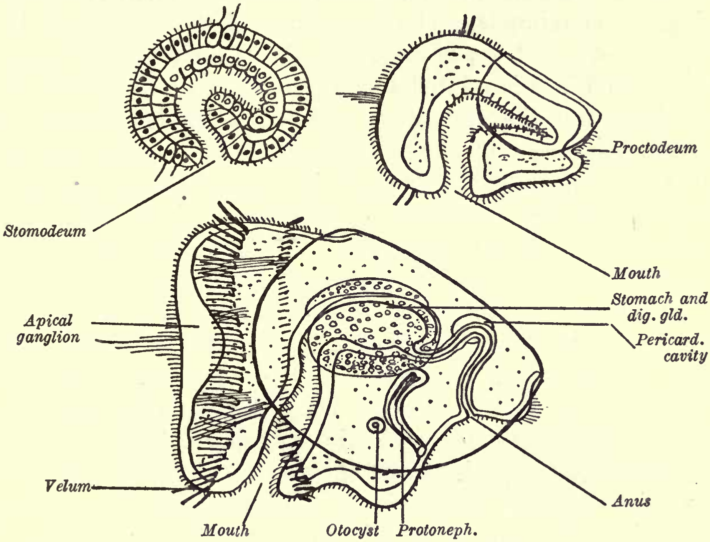


FIG. 36.—Development of trochophore larva of a bivalve mollusc. The endodermal area of the alimentary canal is distinguished from the ectodermal.

occur which are very similar to those of the egg of Annelida. A blastula is converted into a gastrula, and the blastopore of the latter is either converted into the mouth or marks the place where the mouth appears. It is carried inwards by a stomodeal invagination. The foot is produced immediately behind the mouth, thus from the region of the posterior (dorsal) lip of the blastopore. The anus is developed later by a backward growth of the enteron, meeting and fusing with the ectoderm behind the foot. A small ectodermal invagination is formed to meet the enteron, and this is termed the proctodeum. The alimentary canal thus consists of an anterior

large stomodeum and a small proctodeum, both derived from ectoderm, between which the tube consists of endoderm enclosing the enteron. On each side it has been observed in many cases that a protonephridium is formed by an invagination of ectoderm cells, and these end blindly in solenocytes. In this case they are larval organs concerned with the excretion of the schizocoel, as the primitive body cavity is called. They disappear with the development of the pericardial cavity and of the coelomiducts. The resolution of the mesoderm into mesenchyme and a pericardial cavity is an event of importance. The first is related to the primitive space between the ectoderm and the endoderm, and this space is, as has been stated, discharged by the protonephridia.

The primitive circulation of food and oxygen and waste products in the schizocoel or mesenchyme is in the mussel replaced by a blood circulation. The primitive mesoderm or mesenchyme is resolved into free leucocytes which float and move in the fluid plasma and into blood-vessels and a heart. But in the body, in the mantle and the gills, the blood circulates still in indefinite spaces in the mesoderm. The pericardial cavity is a secondary body cavity, separated by a distinct epithelium, the coelomic epithelium, from the primitive body cavity, and is termed the coelom. It is discharged by a special duct, the coelomiduct, which functions as a kidney, but it is to be observed that its function is dependent upon its relationship to the blood. It is aided in its excretionary function by the pericardial glands, the products of which, however, are discharged by the coelomiduct. During these changes the trochophore is converted into a veliger, characterised by the great development of a ring of cilia in front of the mouth. This ring of cilia, the velum, acts in maintaining the larva in the planktonic state and in collecting food, and it is withdrawn when the larva sinks to the bottom (fig. 27). The larva feeds on plankton or suspended matter, as does the adult.

The Mollusca are related intimately to the Annelida, and through the Annelida to the Arthropoda. They are related also to a group which, like the Mollusca, are characterised by a growth behind the mouth, which in them all has a blastoporal origin, and because of this growth we may term them

podectathentous. These are the Rotifera, which do not form a secondary body cavity; the Bryozoa (Polyzoa), or sea mats, which only offer hints of such a cavity; the Brachiopoda, or lamp shells, in which a secondary cavity is well developed, as it is in the Phoronidea and in the Sipunculoidea. The Rotifers possess only protonephridia. In the coelomate forms the protonephridia establish a connexion with the coelom and function as kidneys and gonoducts.

In primitive Mollusca there is an association of pericardial cavity and gonad, and the sex cells of the latter are expelled by the coelomiducts, which are thus kidneys and gonoducts. In the Pelecypoda, as in the higher Mollusca generally, the gonads are separated from the pericardial cavity and acquire separate openings to the exterior, but the tubular gonads are nevertheless coelomic in origin.

CHAPTER V

ANNELIDA

Phylum TROCHOZOA
Sub-Phylum ARTICULATA
Division ANNELIDA

		Types
Class OLIGOCHAETA	. .	Lumbricus
HIRUDINEA		
POLYCHAETA	. .	Nereis

THE Annelida include the earthworms (Oligochaeta), the leeches (Hirudinea), and the bristle worms of the sea (Polychaeta).

The Oligochaeta occur everywhere on land, many are found in fresh water, and a few have obtained a lodgment in the sea near the shore.

Lumbricus.—The common earthworm is *Lumbricus terrestris*. It is common in England and Europe, and nearly allied species and genera are found everywhere. The quantity to be obtained varies with the nature and condition of the soil, but in the soil of lawns, pastures and the like, they are usually present in large numbers. A rough count has shown that over fifty may be found in an area of a square yard. They are therefore of interest to the agriculturist as to the geologist for the share they take in soil formation. The soil is eaten and passed through the alimentary canal, the decaying vegetable matter serving as food, and the residue treated in this way is discharged either below or above ground, above as 'worm casts.' The underlying soil is thus gradually channelled, stirred up, aerated, and brought to the surface; and when the large numbers of the worms are considered and their long history taken into account

it is obvious that their work is, and has been, of considerable importance. They are largely nocturnal in habit, and then may be seen on the surface. Pairing, however, takes place almost at any time of the year, and the worms of adjoining burrows may then be seen attached by the secretion of the clitellum and the capsulogenous glands. The hinder part of the body remains in the burrow, and when disturbed the worms quit their hold of one another and retreat instantly. Worms form the food of many birds and mammals, and are liable to gregarine and other parasites. For further interesting facts relating to the natural history of earthworms consult Darwin's 'Vegetable Mould and Earthworms.'

External Morphology.—The general appearance is familiar. The worm is cylindrical in shape, and posteriorly it is somewhat flattened dorso-ventrally. It is made up of a large number of rings or segments delimited by slight grooves. The segments are capable of extension and contraction by the muscles underneath the skin, and the movements are assisted by the chitinous hooks (chaetae or setae), of which there are eight on each segment except the first and the last. The colour is variable, but the dorsal side is darker, brown to purple, and the dorsal blood-vessel may usually be seen through the thin skin as a dark red line. The saddle, or clitellum, is a conspicuous glandular swelling extending between segments 31 and 37, but varying according to circumstances of maturity and in different species. The capsulogenous glands are similar paired ventral enlargements of the segments, 9, 10, 11, involving slightly also 8 and 12. Some of the openings may be distinguished easily, others with difficulty. The mouth may be seen on the lower aspect of the first segment, and the anus on the last segment. The part of the first segment in front of the mouth is sensory, and is called the prostomium. The fifteenth segment is usually plainly defined by the swollen lips of the opening of the vas deferens on each side. The fourteenth segment bears the openings of the oviducts, for the earthworm is hermaphrodite, but they are minute. Two other openings connected with the reproductive organs are to be found on each side between segments 9 and 10 and between 10 and 11; these lead into sacs called the spermathecae, of which there are two pairs.

The dorsal pores, absent in aquatic types, may be seen by drying the worm with a cloth and stretching it over a finger. This serves to press out some of the fluid of the body cavity. Dorsal pores begin mid-dorsally in the interval between the tenth and eleventh segments, and occur between all the remaining segments to the groove separating the penultimate from the last segment. Each dorsal pore leads into the posterior of the two segments in each case. The nephridial openings, or nephridiopores, begin on the fifth segment, and a pair is found on every segment from that one to the penultimate segment. The openings are difficult to distinguish. They lie one on each side, usually just behind and a little above the lower of the two sets of chaetae.

A thin cuticle is secreted by the ectoderm, and it forms a smooth delicate covering to the skin. It becomes plain if dissection is performed in water, and may then be readily stripped off and examined. It is a hardened exudate of the ectoderm, and the chaetae are of the same nature and are developed in special pockets of the skin, from which they may be protruded and into which they may be withdrawn by special muscles of the skin.

Sections will show that the ectoderm consists of a series of columnar cells forming a single layer, thicker in the middle of the segment and thinner in the grooves. The ectoderm is based on a basement membrane. Glandular cells are interspersed among the columnar cells, and their secretion escapes by pores in the cuticle. In the segments involved in the clitellum the ectodermal cells become largely increased in number and glandular.

Internal Morphology. **Alimentary Canal.**—Like the ectoderm with which it is continuous at either end of the body, the epithelium of the alimentary canal is formed of a single layer of columnar cells. The muscles of the two layers are similar and continuous. Underneath the ectoderm are circular and then longitudinal muscles, the latter continuous and the former interrupted at the grooves. Around the alimentary canal the muscle layers are an inner circular layer and an outer longitudinal layer (fig. 38). If the worm be dissected from the dorsal side it will be found that the alimentary canal

presents the following regions in succession. The mouth opens into a buccal cavity which is protrusible, formed of folds and cavities, and suspended by strands of muscle from the forward region of the body wall which are directed forwards to be inserted into it. The pharynx succeeds as a bulbous region. It is strongly folded on its dorsal side, and its thickness is due to the great development of muscle on its upper side, and it is also supported to the body wall by muscle strands. The oesophagus extends from the pharynx to the thirteenth segment. In the relaxed condition it presents a series of constrictions where the septa encircle it.

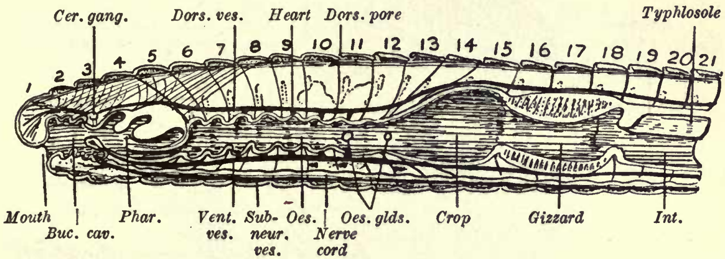


FIG. 37.—*Lumbricus terrestris.* General view of the organisation of the anterior end.

The three pairs of oesophageal glands are swellings of the tube in segments 10, 11, and 12. The first pair open widely into the oesophagus. The others are folded into a series of passages and secrete a milky fluid which is discharged by a duct on each side into the oesophagus, just in front of the crop. These glands may be easily distinguished, besides, by the opaque white lime they contain. The crop is a distension of the tube behind the oesophagus, and it extends to the interval between the fifteenth and sixteenth, when it gives place to the muscular gizzard, and this extends to the end of the nineteenth segment. The intestine leads from the gizzard to the anus, and the tube is similar throughout : it presents a series of slight swellings and constrictions opposite the segments and septa, and the dorsal wall is folded inwards, forming a longitudinal ridge projecting into the lumen. This fold is called the typhlosole. The walls of the intestine, including the typhlosole, are folded,

thus further increasing the surface, and all the endoderm is ciliated.

The earth is taken up by the buccal cavity being protruded in succession through the mouth and the muscular action of the pharynx, which is also rotated forwards and backwards. It is passed along the oesophagus by a series of contractions following one another, an action which is termed peristalsis. It is charged with lime by the oesophageal glands. Harrington [1]

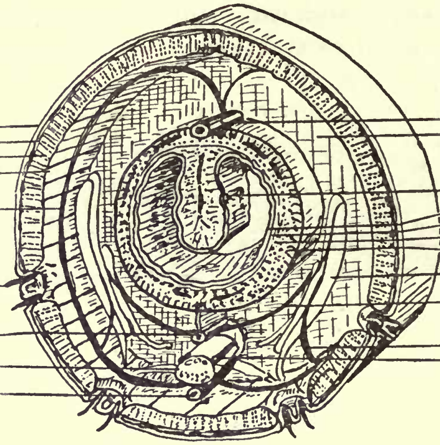


FIG. 38.—Lumbricus. Posterior view of half a segment of the intestinal region.

says that small pebbles of lime are secreted by the first pair and a milky limy fluid by the last two pairs. It is understood that the pebbles are passed along the alimentary canal unchanged and may therefore be excretory, while the fluid lime serves to neutralise the acids of the humus and thus allows of digestion taking place in a neutral or alkaline condition. The food is received by the crop and then passed to be mixed up and pulverised in the gizzard, when it is passed into the intestine for further digestion and absorption. The folds of the typhlosole bring a greater area of endoderm into contact with the food, which is spread into the flattened crescentic space it makes. The anterior end of the alimentary canal is formed

[1] 1899. *Jour. of Morph.* vol. 15.

of invaginated ectoderm—that is to say, the mouth, buccal cavity, and the pharynx—this is the stomodeum. There is also a small proctodeum posteriorly. All the rest of the canal is formed of endoderm and constitutes the enteron.

Body Cavity.—The secondary body cavity, or coelom, is highly developed in the earthworm. It has been exposed in making out the parts of the alimentary canal. The cavity is continuous, but it is interrupted by septa which divide the cavity into nearly separate compartments corresponding with the external rings. The first septum is the posterior one of the fourth segment, and the others occur without interruption to the last segment. The septa are perforated ventrally where the nerve cord passes through them. The body cavity is lined by a thin epithelium or peritoneum. The peritoneum is disposed in a parietal layer internal to the longitudinal muscles of the skin, and each septum is made by the layer folding transversely inwards as a double layer. These diverge from one another to envelop the alimentary canal, and this tubular part is called the visceral layer. The two layers of each septum fuse to form the intercommunicating foramen round the nerve cord. The septum is therefore a transverse mesentery. It has to be observed that none of the organs occurs in the cavity except certain of the generative organs, as will be stated later. The coelom is distended by a fluid, the coelomic fluid, which has amoeboid corpuscles or leucocytes floating in it. The visceral layer of the peritoneum throughout the length of the intestine is tinged yellow, and is thickened from the presence of yellow cells. It was long supposed that these cells took a share in absorbing the food from the enteron, but their function is evidently to abstract waste material from the endoderm and the blood and to cast this into the coelomic fluid for excretion. In the Oligochaeta they are associated with the dorsal vessel and its factors, and they are found also in the Polychaets.

The primary body cavity occupies the little amount of space between the coelom and the alimentary canal on the one hand and the ectoderm on the other. It expands in the anterior end of the earthworm. Elsewhere it forms a connective-tissue system penetrating between the peritoneal

layers of the septa, but it becomes prominent in the blood vessels and the blood.

Vascular System.—The blood is formed of a plasma coloured by haemoglobin and containing colourless leucocytes. Haemoglobin is a complex proteid substance united with iron, and is a respiratory pigment. It has the power of uniting loosely with oxygen, and thus acts as a carrier of the oxygen to all parts of the body of the worm, where it is given up to the organs and tissues, or rather, the cells composing these. Breathing thus takes place in a complex body by the blood conveying the oxygen, in this case from the ectoderm to the most remote parts of the body. The blood as it circulates in the walls of the intestine takes up food material, and this likewise is conveyed to regions where it can be employed for providing energy or for building up and growth. The blood also serves to convey waste material from the cells of the body in general to the excretory organs. The blood is contained in vessels, the larger of which are plainly seen. The alimentary canal is traversed dorsally by a dorsal vessel. In this vessel, which is contractile, the blood runs forwards and the vessel ends anteriorly in branches over the pharynx and buccal sac. During its course it receives vessels from the intestine. It is connected around the oesophagus by five pairs of contractile vessels, called hearts, with a ventral vessel which lies under the alimentary canal. An oesophageal vessel is given off also in the same region, which distributes blood to the lateral walls of the oesophagus and pharynx. The ventral vessel is connected by segmental branches with vessels lying one on each side of the nerve cord, and consequently called lateral neurals, and with a subneural vessel which lies medianly under the nerve cord, and it also supplies the intestine. These are the collecting vessels, and the blood they contain is sent mainly to the nephridia and to the skin. The afferent nephridial vessel passes from the ventral in each segment, and the efferent nephridial vessel enters the parietal. The parietal vessels, one in each segment on each side, pass up the outer wall of the coelom and spread into spaces underneath the ectoderm and into intercellular spaces. The skin is kept moist by the action of the gland cells and by exudation from the dorsal pores,

and thus forms an efficient means of gaseous exchange. The skin is the respiratory organ. The parietal vessels pour their blood into the dorsal vessel (figs. 37 and 38).

Excretory System.—It has already been noted that the yellow cells of the wall of the coelom are concerned in excretion, but the kidneys reach a high degree of development. A pair of nephridia is present in each segment except the first three and the last. The nephridia are derived from ectoderm, and each is a tube which ends in an opening into the coelom. The opening internally is the nephrostome. It is funnel-shaped, and the rim is provided with long cilia which are

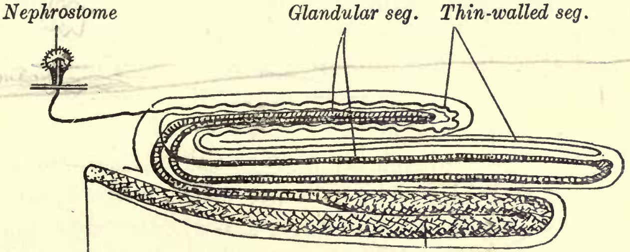


Fig. 39.—Lumbricus. Diagram of nephridium.

incessantly moving. It projects from the anterior face of a septum in each case, and as it pierces the septum it narrows to form a tube the cells of which are bent round to enclose the cavity and are ciliated. This tube is disposed in folds close to the septum, but it is on the opposite side to that containing the nephrostome. It expands into a glandular segment which is likewise folded into loops. The glandular segment is continued into a muscular segment which leads to the nephridopore. The loops formed are complicated, but will be easily followed in fig. 39. The blood-vessels are distributed over the tubes in fine branches and more especially to the glandular segment. It is in this region that the nitrogenous waste material is removed from the blood by the cells, and the coelom provides a head of watery fluid which washes the material to the lower part of the tube. With this in mind, it is clear that the excretion is still to a large extent in the

possession of the primary schizocoel. The mechanical aid of the coelom is called in, and the nephrostome discharges some of the waste products brought by the coelomic amoeboid cells.

Nervous System.—The brain is formed of two cerebral ganglia which lie just above the buccal sac. The brain gives off a large number of fibres to the prostomium. It gives off also the two cords which encircle the alimentary canal in front of the pharynx, the circumoesophageal commissures; these meet below the alimentary canal to form the anterior end of the ventral nerve cord, and this extends to the posterior end of the worm. The cord expands into a ganglion in each segment. Its double nature and origin are indicated by the connective tissue which occupies the middle line of a section. The nerve cells are diffused throughout the cord and give off branches or nerve fibres which leave the cord in bundles called nerves, especially in the segments, and are distributed in serial repetition in each segment to the organs and to the muscles and the skin. The cells are called neurons, and the branches of the cells or nerve fibres axons. On each side of the ventral nerve cord large axons, which have been called giant fibres, are seen in section.

There are no sense organs—eyes, ears, and nose—but the worm is evidently sensible of day and night and of disturbances communicated through the soil.

Reproductive Organs.—The earthworm is hermaphrodite. The sex cells are developed at special places on the coelomic wall. There are two pairs of testes, branched outgrowths of the front septa of segments 10 and 11. They project into the coelom, and the male cells in an immature condition are liberated into the coelom. They are taken up by folds of the septal walls of these segments, and the sacs formed project on each side of the oesophagus as conspicuous white bags. These are the seminal vesicles, and within these diverticula of the coelom the male cells undergo division into balls of cells. The cells then develop flagella, and are thus converted into spermatozoa. The spermatozoa are passed to the exterior by special ducts, the vasa deferentia. From the posterior walls of the tenth and eleventh segments two pairs of funnels are

produced. These lead into ducts which amalgamate to form a pair of vasa deferentia which open to the exterior at the fifteenth segment. The sperms are transferred to another earthworm and stored in the spermathecae. The spermathecae are two

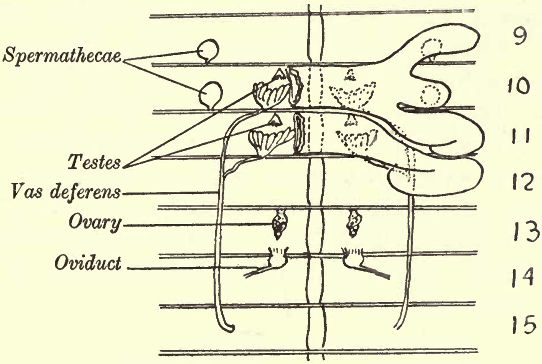


FIG. 40.—Lumbricus. Diagram of reproductive organs.

pairs of ectodermal sacs, which open in the grooves 9–10, 10–11. The two worms approximate from their respective burrows, the head of the one being directed to the posterior end of the other, and lay hold of one another by a double exudation from the clitellum, and their adposed ventral

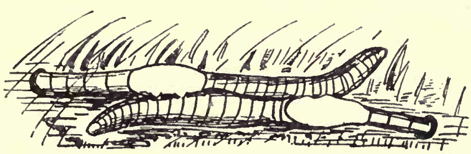


FIG. 41.—Lumbricus. Sketch of worms to show their position in the act of pairing.

surfaces are fixed by the capsulogenous glands. Between the two clitella a groove is thus formed, into which the sperms are discharged by one of the worms and from which they are passed into the spermathecae of the other. It is evident that it is not a matter of exchange.

The female organs consist of a pair of ovaries which are developed from the coelomic epithelium of the front wall of

the thirteenth segment, and, like the testes, they occur ventrally on each side of the nerve cord. The ova as they are matured are passed into the thirteenth segment and led into the opening of the oviduct, which is situated on the posterior wall of the same segment. Piercing this septum the oviduct gains the fourteenth segment, and it opens to the exterior on the wall of that segment. Both the vasa deferentia and the oviducts are developed as outgrowths of the coelom and are therefore coelomiducts. During the process of egg-laying an exudation is passed out from the clitellum. This forms an annular band around the body, and into this the eggs are deposited. As it passes forwards over the worm—the latter retreating all the time—a supply of sperms is liberated by the spermathecae. The mucous band is then passed over the head of the worm and narrows anteriorly in front of the worm; the worm retreating completely from it, the posterior end in turn contracts. The exudate hardens and a capsule containing a few eggs is formed, and this is termed a cocoon. Only one of the eggs succeeds in developing.

The **development** of Lumbricus has been described by E. B. Wilson (1887, 1889, 1891, ' Jour. of Morph.' vols. 1, 3, and 6) and by Hoffmann (1899, ' Zeit. wiss. Zool.' Bd. 66), and of the parasitic Bdellodrilus by G. W. Tannreuther (1915, ' Jour. of Morph.' vol. 26). The early stages are very similar in Annelids, Mollusca, and Rotifera, and resemble those of the Turbellaria. The segmentation is unequal, and the fate of the primary cells, A, B, C, D, similar in all. The gastrula is formed by the ectoderm cells, which are the smaller, growing over the endoderm and the mesoderm, which latter is early separated. This process is known as epiboly, but in Lumbricus it is accompanied by invagination. The blastopore narrows by the fusion of the ectoderm cells. In Lumbricus it forms the mouth. In Bdellodrilus it closes, but the point marks the place of origin of the stomodeum and mouth. The proctodeum appears later, after the embryo has made considerable progress in length. The ectoderm cells give rise to the ectoderm, nervous system, and nephridia (even evidently the nephrostomes), the endoderm cells to the endoderm, and the mesoderm cells to the mesoderm. The whole of the

mesoderm, both primary and secondary, may thus be formed, but the ectoderm may contribute to the former. Mesenchyme cells are budded off which give rise to the products of the primary body cavity, and the rest of the mesoderm forms the

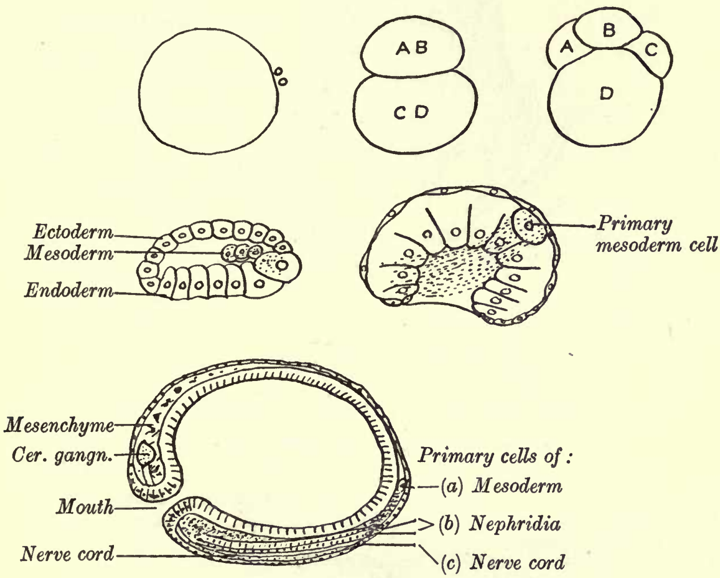


FIG. 42.—Lumbricus. Developmental stages, after Wilson. The first three figures illustrate the remarkably constant manner of segmentation in Oligochaets, Mollusca, Rotifera, and other Trochozoa. The view in each case is a dorsal one: B is anterior, D is posterior, A is left and C is right. The remaining figures illustrate, 1, the flattening of the blastula and the position of the special product of D relegated to form the mesoderm; 2, the gastrula, and by dotted lines the extension of the mesoderm on each side of the enteron; 3, the blastopore narrowed to be carried in by the stomodeal invagination, the final opening to the exterior being the mouth. The last figure also indicates the position of the mesodermal band, the nephrogenous band, and the neuroblastic band, which are all paired.

coelom. It is at first solid, but as it grows and spreads spaces appear which fuse to form the coelom, and the nephridia also become hollowed out and establish openings into it, the procedure going on from the anterior to the posterior end. The anterior ones are protonephridia with solenocytes which project into the head schizocoel, not into the coelom, and they are developed from special ectoderm cells in the region of the dorsal

lip of the blastopore. The nephridia are developed like protonephridia, but from a special ectodermal nephrogenous

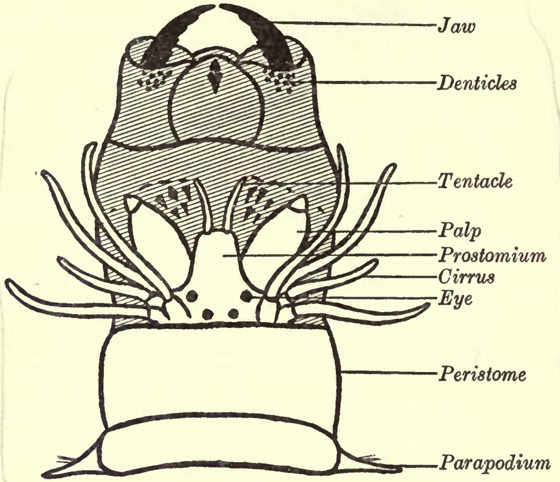


FIG. 43.—Head of *Nereis diversicolor*.

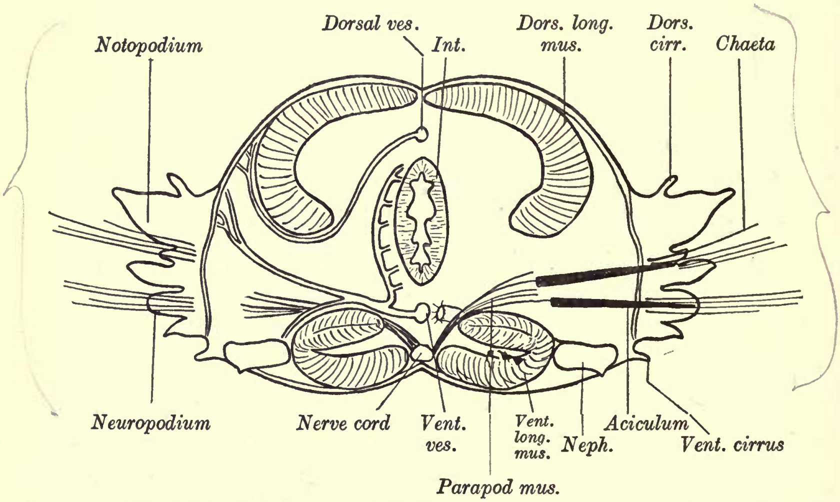


FIG. 44.—Section of a segment of Nereis. (After McIntosh.)

band, and are converted into nephridia by developing an opening into the coelom. As the body grows in length, which

it does from a region just ventral to the proctodeum, the endoderm is hollowed, if necessary, to produce the enteron, the nervous band is expanded into segmental ganglia—the cerebral ganglia are formed from their anterior ends—and the coelom is divided by the formation of the septa, and at the same time distended by coelomic fluid. Growth in length is associated with special cells derived from the posterior end of the ovum and the dorsal lip of the blastopore. These yield the mesoderm and the ectoderm; the mesoderm and the nerve cord and nephridia in special band-like series of cells. The bands become differentiated in front while they are being formed posteriorly.

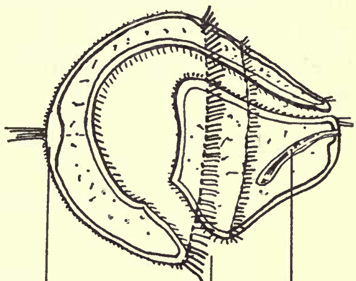


FIG. 45.—Trochophore larva of a Polychaet. Compare with fig. 36.

Nereis.—It may be convenient to examine a species of the marine bristle worms. The genus Nereis is common between tide-marks. It will be noted that the Polychaet differs from the Oligochaet by having the lateral body wall in each segment produced into parapodia bearing many bristles or chaetae. A closer inspection will show that the parapodium divides into a dorsal notopodium and a ventral neuropodium, that each is bilobed and bears a process called a cirrus. The mouth is on the first segment, and it leads into a protrusible buccal cavity and this again into a pharynx. At its anterior end the pharynx is armed with two strong chitinous jaws, and the buccal sac bears many small denticles. The prostomium is furnished with two pairs of eyes and bears processes known as palps and tentacles (fig. 43).

General Considerations.—Marine worms often have a larval stage in development. The larva is a trochophore and is very similar to that of the Mollusca. It consists of an ectoderm and an endoderm communicating at a mouth and anus with the exterior, and is furnished with one or more rings of cilia. The mesoderm is primary, and the cavity is a primary body

cavity into which a pair of protonephridia are thrust from the ectoderm as excretory organs. They are sometimes branched into two, and the branches end blindly, as usual, in solenocytes. The secondary mesoderm and the coelom appear only during the conversion of the larva into the worm, and the nephridia are developed then: they are ectodermal in origin and, as in Lumbricus, are put into communication with the coelom. In some Polychaets they act also as gonoducts.

The Podectathenta are very similar in their history, but in them the coelom remains simple and the space is primarily a gonocoel. Protonephridia are developed in relation to the schizocoel in front of the coelom, and appear in all cases to be converted into the nephridia of the adult, where they act also as gonoducts.

CHAPTER VI

CRUSTACEA

Phylum Trochozoa
Sub-Phylum Articulata
Division Arthropoda
Class—

Crustacea	Land, fresh water, sea. *Type,* Nephrops.
Trilobita	Extinct, sea.
Merostomata—	
Xiphosura	Sea.
Eurypterida	Extinct, fresh water, sea.
Pycnogonida	Sea.
Arachnida	Land, fresh water, sea.
Tardigrada	Fresh water, sea.
Prototracheata	Land.
Myriopoda	Land.
Insecta	Land, fresh water, and rarely sea. *Type,* Blatta.

We have reason to believe that the Annelida have an ancient history, but the hard skeletons of the Mollusca and of the Articulata which have been preserved in the formations show that many of the classes of the Trochozoa were in existence at the dawn of palaeontological history.

The Annelida have segmented bodies. The Arthropoda have segmented bodies and segmented limbs.

Nephrops.—The Norway lobster, also sometimes called the ' crayfish ' and the ' prawn,' is very common in the deep water a few miles from the coast in several parts of the North Sea, Irish Sea, etc. It is common on the coast of Norway,

and it is obtained as far south as the Mediterranean. Unlike its ally, the common lobster, it occupies soft or muddy ground. Norway lobsters are caught by trawlers at all seasons, and may be obtained at most of the markets.

At a glance it is seen to be very like the common lobster and the crayfish and other long-tailed Decapod Crustaceans. Like these, moreover, it crawls by the action of the walking legs forwards and backwards, and shares with many of them the power of swimming backwards at a very rapid rate by strong, rapid contractions of the abdomen. The force exerted may be estimated when the living animal is held in the hand. The diet is almost, if not quite, a purely animal one. The food is seized by the long pincers, or chelae, and conveyed by the foot-jaws or maxillipeds to the mouth.

Growth takes place by a series of ecdyses or moultings, but it has been observed exceptionally that ecdyses may occur without growth apparently resulting. At each ecdysis the whole of the cuticle and the parts internally continuous with it are thrown off or 'cast.' The ecdyses occur very frequently at the beginning of growth, and then also more frequently in the summer than in the winter ; but the periods, called instars, between them become more and more extended, concomitant with the slowing down in the intensity of growth, which ceases when the animal reaches a size of some eight to ten inches. The limit of size, however, is not quite the same in every locality, and may vary, indeed, in the same locality.

All the appendages may be regenerated when lost, and the pereiopoda may be automatically thrown off at the 'breaking joint' near the base of the limb.[1]

As a rule, the external cuticle of the Norway lobster is not much subject to the commensal attachment of other animals, but in some cases certain zoophytes obtain a lodgment.

External Morphology.—The body, which is light red in colour, is divided into a cephalothorax and an abdomen, each with a definite number of appendages. The head consists of five segments, the thorax of eight segments, and the abdomen

[1] 1915. Paul, *Autotomy among the Decapod Crustacea.* Report, Dove Marine Laboratory. New Series, IV.

of seven segments. The segments of the head and thorax are fused together; these regions of the body are also fused and protected by the cephalothoracic shield or carapace. The thoracic portion of the latter is formed by an outgrowth of the hinder region of the head fusing with the dorsal portions of the thoracic segments, and it extends downwards on each side to protect the gills. The distinction between the head and the thorax is indicated by the cervical groove. The cephalothorax is produced anteriorly into a rostrum armed with three or four pairs of dorso-lateral spines, and one or two median spines antero-ventrally, all of which are brought into use during ecdysis; the rostrum is fringed with hair-like processes (setae) on each side. A depression on each side of the rostrum receives the stalked movable eyes, which are large and of the reniform shape which has suggested the generic name. Branchiocardiac ridges provided with small pointed projections divide the thorax into a median cardiac region, and the gill-covers or branchiostegites. On both head and thorax there is a median dorsal ridge bearing small points, other depressions and ridges, and on the head there are series of spines.

The abdomen consists of seven segments, articulated to one another at each side, and connected by thin uncalcified portions of the integument. Each presents a beautiful regular pattern produced by elevations and depressions, and each, with the exception of the last, bears a pair of appendages. The last segment forms the median element of the tail or paddle, the other contributing elements on each side being the modified and highly developed appendages of the sixth segment.

The limb-bearing segments of the abdomen each consist of a dorsal strongly curved plate, the tergum, produced downwards on each side to form the two pleura, of a ventral sternum between the appendages, and of the epimera between the appendages and the pleura on each side. The pleura are absent from the first segment.

The females are smaller than the males, and in the female the abdomen is broader, the pleura being more obliquely placed.

The appendages are:

Head. Antennules, or Anterior or First Antennae.
Antennae, or Posterior or Second Antennae.
Mandibles.
1st Maxillae.
2nd do.

Thorax. 1st Maxillipeds.
2nd do.
3rd do.
Pereiopoda, or Walking Legs—five pairs, the first pair being the Chelae, or pincers.

Abdomen. Pleopoda, or Abdominal Appendages—six pairs.
The sixth pair of abdominal appendages are called Uropoda. The last segment, the telson, bears no appendages.

The appendages typically consist of a basal portion or peduncle (protopodite) bearing two rami (exopodite and endopodite), but they are more or less modified according to the position they occupy and the function they perform.

The antennule consists of a three-jointed peduncle (protopodite) bearing two sub-equal flagella. The outer flagellum (exopodite), is slightly thicker than the inner (endopodite). The basal segment of the peduncle is longer than the other two together; the proximal part of this segment is expanded and contains the auditory sac. The flagella function as tactile and as olfactory organs.

The antenna is made up of a two-jointed peduncle (protopodite) bearing a flattened antennal scale externally (exopodite) and the long feeler (endopodite). This latter consists of three basal segments (peduncle of flagellum) and the long flagellum, made up like the flagella of the antennules of a large number of very short segments. The flagellum is tactile. The first segment of the protopodite presents on its ventral surface a prominent tubercle bearing the opening of the antennal or green gland; the second or distal segment is produced externally into a process.

The mandible, the first oral appendage, is very much

Endoske apodemes: I

modified. It consists of a strong, hollowed, unsegmented body (protopodite) attached on its outer edge to the body

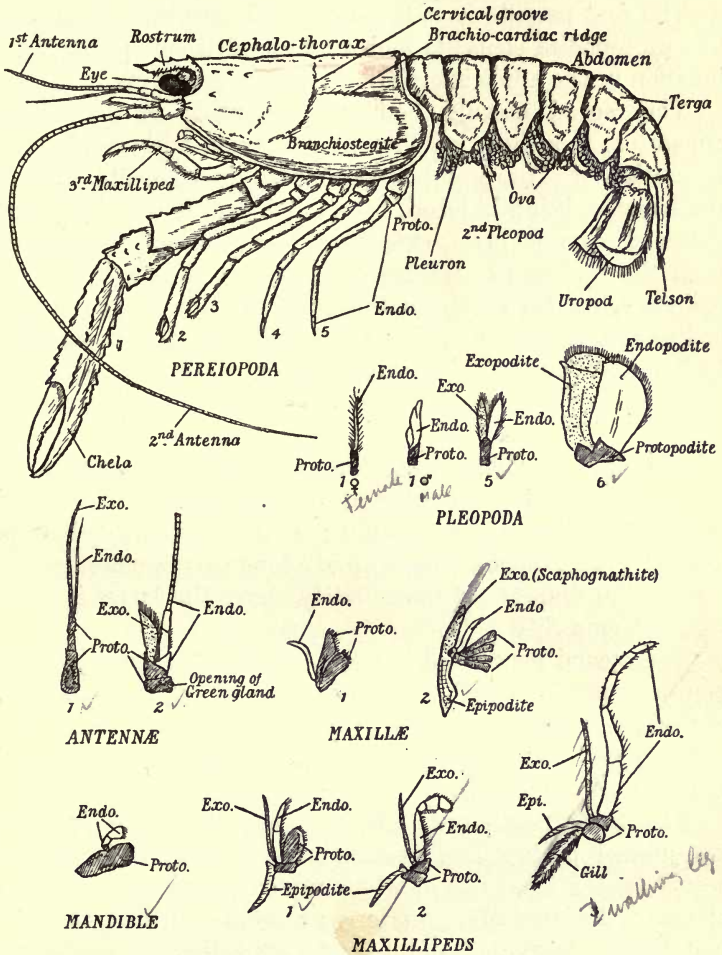


Fig. 46.—Nephrops. External characters of female. Below, the appendages of the right side are shown (except the pereiopods).

wall, and ending distally in a process bearing chitinous teeth. Between this and a horizontal shelf is a cavity in which the thickened front lip (labrum) is received. On the outer edge

is borne a three-jointed palp ; the first of its segments is believed to belong to the protopodite, and the other two to form the endopodite.

The first maxilla is rudimentary and consists of two leaf-like protopodite elements and a two-jointed endopodite. Its function in the adult is probably quite unimportant.

The second maxilla, besides contributing to the mouth apparatus, is greatly modified in connexion with respiration. It consists of (*a*) a protopodite of two thin segments, each of the lamellae being bi-lobed, (*b*) an endopodite, and (*c*) a long flattened curved plate extending forwards and backwards from the surface of attachment in the cervical canal. This plate is called the scaphognathite, and is made up of the exopodite and an element allied to the gills called the epipodite. In life it is constantly in movement, and in such a manner as to bring about a forwardly moving current of water over the gills.

The first maxilliped is the smallest and consists of (*a*) a small basal and a large distal segment internally, and forming together the protopodite; (*b*) a two-segmented endopodite; (*c*) an exopodite made up of a long narrow plate bearing a short flagellum; and immediately above the latter is (*d*) a thin flat epipodite.

The second maxilliped is made up of a two-jointed protopodite supporting a well-developed endopodite of five segments, a thinner rounded exopodite, and a small epipodite. The latter is attached to the basal element of the protopodite and lies in front of the gills.

The third maxilliped, like the preceding, consists of a two-jointed protopodite, bearing a large endopodite of five segments, the basal one of which presents a row of teeth-like spines on the inner edge anteriorly ; a small exopodite, rounded and distally flagellate ; and a slender epipodite.

The last five pairs of thoracic appendages, the pereiopoda or walking legs, are characteristically well developed in the 'Decapoda.' They agree with one another in consisting of a two-jointed protopodite and a five-jointed endopodite. The exopodite is suppressed, but it is present in the larva. The first three are chelate and the last two simple. The basal

segment of the protopodite has been named the coxopodite, and the distal segment the basipodite. Similarly the five segments of the endopodite have been called in succession, beginning at the proximal end, ischiopodite, meropodite, carpopodite, propodite, dactylopodite. The chelate condition arises by the propodite being prolonged beyond the articulation of the dactylopodite, so that the latter comes to be articulated antero-laterally instead of distally. The first pair, the claws, pincers, chelipeds or chelae, are much longer and stronger than any other pair, and one is ordinarily rather larger than the other. They are used for tearing the food, and also for offence and defence. The basipodite and the ischiopodite are fused together in the first pair. The oviduct of the female opens on the basal segment of the third pereiopod, and the vas deferens of the male on that of the fifth pereiopod. But the openings are subject to variation, abnormal specimens being occasionally obtained with more than one pair of openings. For instance, in the male there may be additional paired or unpaired openings on the fourth and even on the third pereiopoda. In the female a fold between the third pereiopods forms a chamber for storing spermatophores, and is therefore a spermatheca.

The first of the pleopoda, or abdominal appendages, is modified in both sexes. In the male it is in the form of a firm, irregularly cylindrical rod projecting forwards between the bases of the last pair of pereiopoda. Each is formed of the fused protopodite and endopodite, the exopodite being absent. The endopodite is folded so as to form a gutter-like groove. The posterior end of the groove can be applied to the opening of the vas deferens, and the gutter serves to convey the spermatophores to the spermatheca of the female. In the female the first pair are long and thin, and each consists of a two-jointed protopodite, and a jointed setose filament which is believed to be the endopodite. They share the function, with the next four appendages, of supporting the eggs during the long incubatory period. The second pair of appendages of the male are also modified and somewhat larger than those of the female, the endopodite being produced on its inner border into a long flat plate, doubtless of use in supporting

H

the first or penial pair. In the female, the second pair have the same structure as the next three. The third to the fifth have all a similar structure in both sexes, but they are larger in the female than in the male. They each consist of a two-jointed protopodite bearing two flattened oval setose plates, the endopodite and the exopodite. The sixth abdominal appendages, the uropoda, are highly developed, but they consist nevertheless of a strong broad protopodite, produced dorsally into an outer and an inner spine, and of the two large plates on each side of the telson. These are the endopodite and the exopodite, and the latter is subdivided near its extremity by a transverse joint. The joint is further distinguished by the row of small spines on the distal edge of the large basal portion.

The Gills.—The gills are borne by the appendages of the thorax and the segments corresponding to them. They are outgrowths of the integument, and each consists of a slender column, containing the two blood-vessels and bearing a dense mass of branchial filaments arranged for the most part in two rows. They project upwards, side by side, in the branchial chamber (formed by the downgrowth of the carapace—the branchiostegite), each segmental group being separated from the next by the epipodite. They are arranged in three layers: (1) the outer series, the podobranchs, borne by the proximal segment (coxopodite) of the appendage in each case; (2) a middle series, the arthrobranchs, arising from the thin integument forming in each case the joint between the limb and the body; and (3) an inner series, the pleurobranchs, attached to the body wall.

The gill formula of the Norway lobster is:

	Maxillipeds			Periopods					Totals
	1	2	3	1	2	3	4	5	
Podobranchs	ep	ep	1+ep	1+ep	1+ep	1+ep	1+ep	..	5 gills 7 ep
Arthrobranchs	..	..	2	2	2	2	2	..	10 gills
Pleurobranchs	..	..	..	..	1	1	1	1	4 gills
Totals	ep	ep	3+ep	3+ep	4+ep	4+ep	4+ep	1	19 gills 7 ep

Each podobranch arises from the base of the laminar

epipodite. The arthrobranchs occur in pairs, on the joints of the segments indicated. The four pleurobranchs are the largest gills in the Norway lobster, but in the fresh-water crayfish, for example, they are rudimentary, except the last. The scaphognathite, or baler, the lamellar expansion of the second maxilla, which lies in the cervical canal in front of the gills, serves by its constant movement to draw a steady current of water through the gill chamber. The current passes from behind forwards, and thus brings about the respiratory

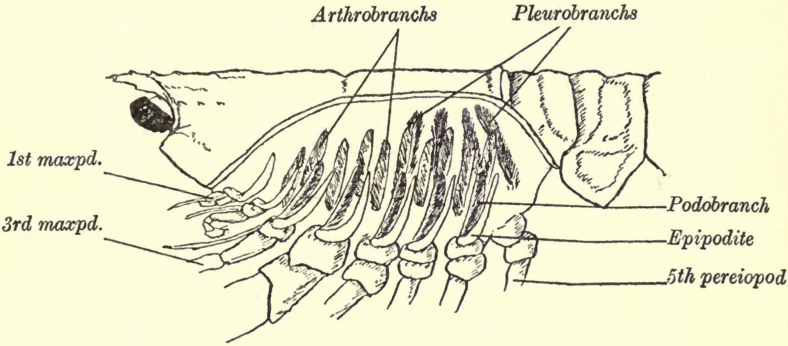


FIG. 47.—Nephrops. The gills displayed by the removal of the branchiostegite of the left side.

exchange and the washing out of excretory products from the gills.

INTERNAL MORPHOLOGY.—The integument consists of the ectoderm and the chitinous cuticle which proceeds from it. The ectoderm is supported on a basement membrane, beneath which is a connective-tissue layer, bearing nerves and containing pigment. The cuticle is hardened in segments by the deposition of lime salts. It is uncalcified or soft at the joints, on the inside of the gill covers and also on the gills themselves. It may usually be resolved into four layers: (1) an outer, thin, non-calcified layer; (2) a calcified pigmented layer formed of parallel lamellae; (3) a calcified non-pigmented layer, usually the thickest, also formed of parallel lamellae; (4) a thin non-calcified layer, also made up of lamellae. The cuticle arises by the successive thickenings of the outer portion of the ectodermal cells; this gives the lamellated structure, and

the divisions between the cells account at the same time for the prismatic appearance and the pores.

The integument also forms the skeleton, and in relation to the muscles it is produced inwards to form so-called tendons (apodemata). Such internal projections of the cuticle form a complicated endophragmal skeleton on each side of the floor of the thorax, a skeleton which serves for the attachment of the prominent muscles of the legs and the flexor muscles of the abdomen; it also forms a canal for the ventral nerve cord.

Muscular System.—The muscles of the body and the limbs are striated and white in appearance. They are especially well developed in the abdomen and the chelae. They are attached to the basement membrane, and the thin ectoderm therefore intervenes between them and the cuticle. As has already been pointed out, internal foldings of the cuticle are developed in relation to many of the muscles, and in some cases, as for example the adductor muscle of the mandible and the strong muscles of the chelae, the internal process is long and tendon-like. In the abdomen the muscles are symmetrically disposed on each side, and consist of a dorsal pair originating from the side wall of the thorax and dividing into a series of bundles which are inserted in succession into the various terga, and of a stronger ventral pair originating from the upper part of the endophragmal skeleton, which similarly divide to be inserted into the sterna. The segments of the abdomen are articulated by joints at the sides. The dorsal pair, therefore, act as extensors and the ventral pair as flexors. The muscles of the appendages pass from their origin on the inside of the segment in each case to be inserted into the edge of the next segment. There are important muscles also in relation to the stomach.

Alimentary Canal.—This consists of a short oesophagus, a large two-chambered stomach and a straight intestine. The inner layer secretes a lining of chitin continuous with the external cuticle at the mouth and anus, except in the small anterior portion of the intestine into which the bile ducts open. Thus the digestive tube may be divided into a fore-gut or stomodeum, including the oesophagus and stomach,

lined with a chitinous cuticle, and derived from a secondary invagination of the ectoderm; a mid-gut or enteron, representing alone the primitive enteron of the embryo and from which the paired digestive gland originates; and a hind-gut or proctodeum—practically the whole of the intestine—developed from an ingrowth of the ectoderm.

The Stomodeum.—The mouth is a V-shaped opening, a vertical fold of the anterior lip, or labrum, projecting backwards into the cavity. It is bounded at the sides by the mandibles.

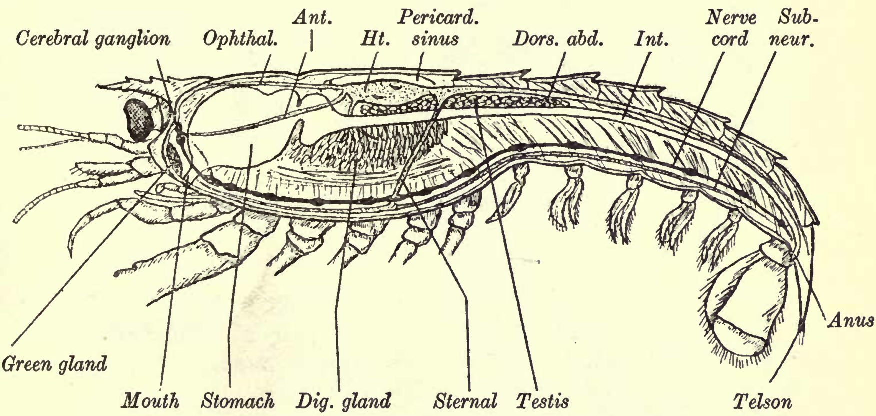


FIG. 48.—Nephrops. Median longitudinal section of male.

The red-coloured gullet is very short, and opens into the capacious stomach. The latter consists of a large cardiac chamber and a smaller pyloric chamber. It is lined by a transparent chitinous cuticle, thickened along definite lines to provide sclerites for the attachment of muscles and the grinding of the food. It is also produced into setae, which act as filters. On the roof of the stomach a combination of the sclerites produces the gastric mill. The ossicles entering into its formation form virtually a hexagonal framework provided with teeth. The cardiac ossicle is a transverse bar on the top of the cardiac chamber. The roof of the pyloric chamber is similarly provided with a shorter compact sclerite, the pyloric ossicle. These two ossicles are joined by two short median pieces; the anterior of these is the precentral ossicle or urocardiac,

and the posterior, the post-central ossicle or prepyloric ; and the latter is produced to form the median tooth which lies at the bottom of the depression between the two gastric cavities. On each side of the cardiac is articulated a small curved prelateral ossicle or pterocardiac. Between the prelateral and the pyloric on each side, and articulating with the latter through the intervention of a small exopyloric, is the large post-lateral ossicle or zygocardiac, which is bent downwards into a strong, serrated lateral tooth. The muscles

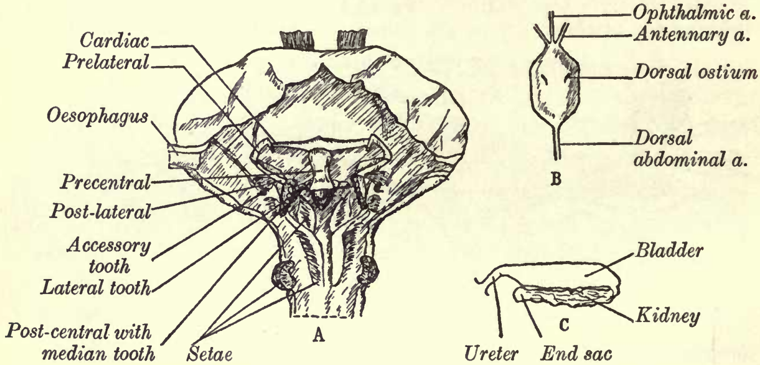


FIG. 49.—Nephrops. A, gastric mill, ventral view ; B, heart from dorsal side ; C, green gland.

which put this apparatus into motion are principally a pair which stretch forwards from the cardiac region of the stomach to the carapace, and a pair which pass backwards from the pyloric region, also to the carapace. When these contract, the lateral teeth are pulled inwards and upwards, and the median tooth at the same time is drawn upwards and backwards ; and when the muscles are released these movements are reversed. In addition to the sclerites mentioned, two accessory lines may be seen extending forwards and backwards from the junction of the pre- and the post-lateral on each side. The hinder one ends in a distinct round ossicle bearing two or three small teeth. Setae are developed in relation to a ventral pair enclosing a groove just behind the gullet. Other hardened lines may be distinguished in the

pyloric region, with fine hair-like setae, projecting from pouches and depressions, and these act as a sieve. The chitinous cuticle of the stomodeum ends posteriorly in a series of processes, and it is shed and renewed at every ecdysis.

Glands are situated in the walls of the oesophagus, and their ducts are continued through the chitinous layer. They have been called salivary glands.

The mid-gut, or enteron, is the very short region succeeding the stomach. It is free from a chitinous lining, receives on each side the duct from the digestive gland or liver which is a paired expansion of the enteron, and its roof is produced into a small caecum. The digestive gland or liver is very large ; it lies on each side of the stomach and extends as far back as the beginning of the abdomen. It is made up of a mass of small glandular tubes, which open ultimately by a single duct on each side into the mid-gut. The mid-gut and the digestive gland together form the digestive and absorptive region of the alimentary canal. The gland is provided with special large vacuolated cells which furnish the digestive ferments, and fat cells for the storage of glycogen and fat. The products of digestion are also absorbed by the digestive gland, but the fats may be absorbed to some extent by the mid-gut. The gland appears to be able, moreover, to arrest poisonous substances, and to share with the excretory organs the regulation of the quantity of the blood plasma. It has an excretory function as well, yielding yellow, brown, or green pigment.

The hind-gut, or proctodeum, is a straight tube lined throughout by a thin chitinous cuticle and opening on the ventral side of the telson. Intestinal glands occur with ducts leading through the cuticle, and are very similar to the so-called salivary glands. This chitinous cuticle of the hind-gut is also shed at each ecdysis.

Circulatory System.—The blood consists of a plasma containing a pigment, haemocyanin (a proteid united with copper), and corpuscles of two kinds, both colourless, (1) leucocytes and (2) thrombocytes. The former are like the white corpuscles of the blood of vertebrates. The latter are usually spindle-shaped as in other animals, and have the peculiar

property, when the circulation stops, or when the blood escapes, of becoming round and viscous peripherally, increasing in size at the same time, and throwing out long filamentous pseudopodia, in which an active circulation of granules may be witnessed. The pseudopodia fuse with one another and entangle neighbouring cells, thus forming a plasmodial clot.

The blood flows in the spaces around the tissues and organs ; these sinuses or lacunae culminate in the large ventral or sternal sinus in the ventral part of the thorax ; from the ventral sinus the blood is sent to the gills, and from the gills to the pericardial sinus in the upper region of the thorax ; the heart is moored in the middle of the pericardial sinus, from which it receives the blood through the ostia and transmits it once more to the body. The heart is attached to the carapace by fine muscular threads on each side, and lies otherwise freely in the pericardial sinus. It is sub-hexagonal in shape, and its muscular wall is perforated by six apertures—the ostia—two dorsal, two lateral, and two ventral (fig. 49, B). These admit the blood from the pericardial sinus, and the thin lip-like pair of valves with which each is provided prevents the blood from passing outwards during contraction. The heart beats twenty to thirty times a minute, and propels the blood into the arteries. Anteriorly three vessels leave the heart close together, a median one, the ophthalmic, and the paired antennary arteries. The former passes forward over the stomach and bifurcates to supply the eyes and the front of the stomach. Each of the antennary arteries runs along the side of the stomach, giving off gastric branches, and, reaching the front of the stomach, it supplies the antennae, the antennules, the rostrum, and the green gland. The heart also yields anteriorly from its ventral surface the paired hepatic arteries to the digestive gland. At the posterior end of the heart a vessel arises and immediately divides into (1) the median, dorsal abdominal, which runs backwards along the dorsal side of the intestine, giving off branches in each segment to supply the muscles, intestine, etc. ; and (2) a sternal artery, which passes directly downwards and, passing between the commissures which unite the third and fourth pereiopod ganglia, divides into the anterior and posterior sub-neural arteries, which yield paired branches to

the appendages, and supply also the parts in their neighbourhood.

The arteries divide into smaller arteries or even into arterial capillaries, and these empty their blood into the lacunar spaces or sinuses. The blood finds its way, in the sinuses up the appendages along the dorsal and ventral abdominal sinuses, from the various regions of the cephalothorax, to the large ventral sinus of the thorax. On each side of this sinus, where

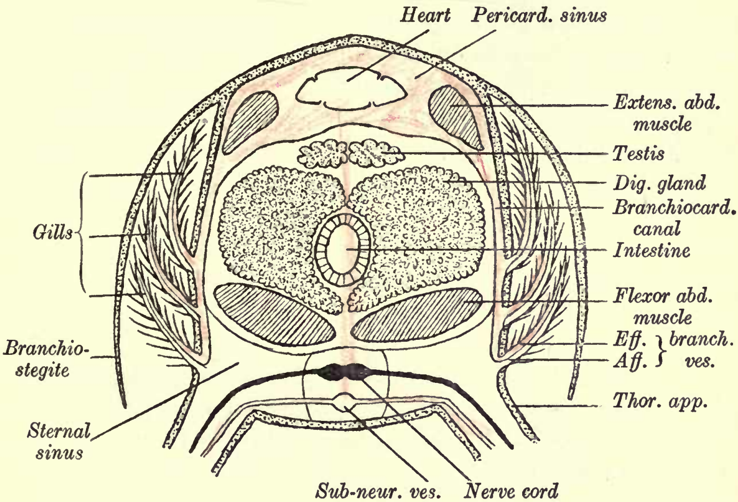


FIG. 50.—Nephrops. Transverse section through thorax, modified after Parker.

the pereiopod sinuses open, are a series of apertures leading into the gills by the afferent branchials. These run in each case up the outer side of the column of the gill and into the filaments. The blood is brought back from the filaments by the efferent branchials which run down on the inner side of the column of the gill to open into the branchiocardiac canals. The latter convey the arterial blood up the side of the wall of the thorax to the pericardial sinus.

Body Cavity.—The cavity between ectoderm and endoderm and surrounding the organs is the primary body cavity expanded as a haemocoel. The coelom is present in the embryo as a series of cavities, as in the Annelids, but this mesoderm

degenerates, forming the striated muscles. The cavities of the gonads and the end sac of the green gland alone survive as coelomic cavities. Their ducts are mesodermal in origin, and are therefore coelomiducts.

Nervous System.—The nervous system consists of a brain, the cerebral or supra-oesophageal ganglion, connected with a ventral chain of ganglia. The brain is placed on the front wall of the head between the eyes. It gives off paired nerves to the eyes, to the antennules and to the antennae, and is connected with the ventral chain by two long oesophageal commissures, which pass backwards on each side of the oesophagus to unite in a large sub-oesophageal ganglion. The latter is made up of the fused ganglia of the segments represented by the mandibles, maxillae, and the first two pairs of maxillipeds. The ganglion representing the third maxilliped segment immediately succeeds the sub-oesophageal ganglion, and then follow the five ganglia of the pereiopod segments, and the six abdominal ganglia. The ventral ganglia receive and transmit impulses affecting their own segments, but they are all under the co-ordinating control of the brain.

In addition to the ganglia and the nerves associated with them, there is a visceral or so-called sympathetic system. This consists of two nerves passing backwards from the brain, internal to the oesophageal commissures, to the oesophagus, and supplying the stomach, liver, and perhaps also the heart.

The large reniform compound eyes are situated at the ends of the movable eye-stalks. The latter are sometimes considered a first pair of appendages, and it is remarkable, at all events, that when the whole eye-stalk is artificially removed an antenna grows in its place. Each eye consists of a large number of similar elements, or ommatidia, radiating outwards from the optic ganglion at the end of the optic nerve. The nerves proceeding from the ganglion pierce a basement membrane and enter the basal sensory elements of the ommatidia—the spindle-shaped, striated rhabdome, made up of four cells enclosed by the retinula cells. The rays of light are transmitted in each case by the crystalline cone of four cells, which end in a point internally, the corneal ectoderm and the flat square facet of the transparent cornea. The cornea is shed at

every exuviation. The ommas are surrounded by pigment cells designed to absorb or reflect the rays. The black or dark brown absorptive pigment varies with the intensity of light. It is not yet quite clear as to how the image or images are built up by the eye as the instrument intervening between the brain and the external objects. The ommatidia are so disposed that they cannot all see the same object at once,

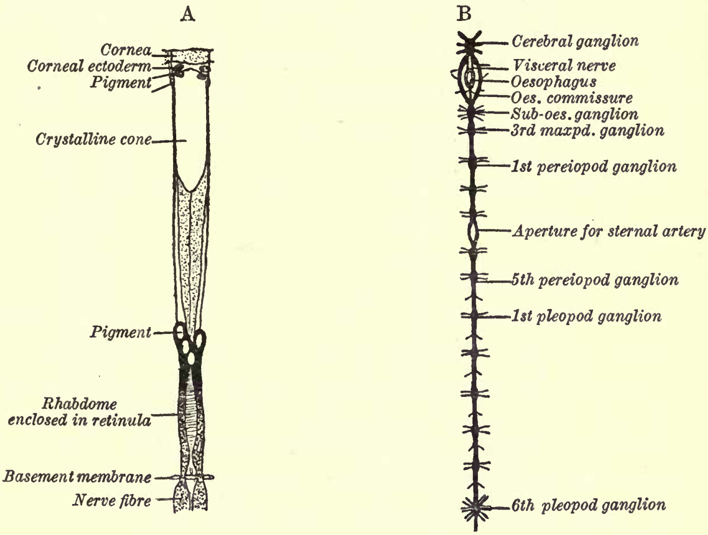


FIG. 51.—Nephrops. A, a single element, ommatidium of the compound eye; B, nervous system. After G. H. Parker.

and an all-round picture of a wide range is more or less perfectly conveyed to the brain by the two eyes. They have been compared, or the assemblage of rhabdomes, to the rods and cones of the vertebrate eye, and it may be imagined that the picture is built up by each omma contributing as much as lies in its way. If perfectly fresh eyes be held in a favourable light, it will be found that the outer layer of pigment does not prevent one seeing through the layer of crystalline cones. In such a case the single reflected images of external objects may be seen within the eye, occupying, according to distance, more or less of the inner part of the layer of crystalline cones. If the eye be placed under the microscope, and the

cornea focussed, it will be found that a very sharp image of a moving object, such as a pencil held in the hand, can be obtained by lowering the microscope tube so as to bring the rhabdomes into focus.[1]

The auditory organ in the basal segment of the antennule is a sac-like ingrowth of the integument, containing a watery fluid, and furnished with setae and small concretions. The setae are connected with the antennule nerve, and appear to be the means of transmttiing vibrations to the brain. The organ also is associated with co-ordinating movements, with the sense of position, and maybe also with the homing instinct. The antennules perform what in the water answers to the olfactory function.

Excretory Organs.—The green gland, or antennary gland, is a coelomiduct. It consists of an end sac, the reduced coelom, a plexus of tubules forming the glandular portion, a wide bladder and a ureter, the latter ending in the pore on the basal segment of the antenna (fig. 49, C). The glandular part has an alkaline reaction, and the green colour is due to the guanin which with uric acid has been shown to form part, at least, of its excretory products. Excretion appears also to be shared by the groups of cells found in the gills (branchial glands) and by the liver. The cuticle shed at ecdysis may also be recorded as an excretion. The branchial glands are probably environment organs (p. 130).

Reproductive Organs. Male.—The testes consist of two long, straggling, irregular-folded lobes, extending from the stomach to the beginning of the second abdominal segment. They are joined together just beneath the heart, and from that region the vasa deferentia pass out as slightly coiled tubes to open in each case on the basal element of the last pereiopod. Each vas deferens is made up of a short, narrow, coiled portion, a dilated glandular middle part, and a muscular region. The spermatozoa have a rather remarkable appearance. They consist of a nucleated central portion produced into one long, usually straight, process, homologous with the flagellum of the flagellate sperm, and three smaller curved processes derived from the neck; that is to say, between the flagellum and the

[1] 1910. Demoll, *Ergeb. und Fortschritte der Zoologie*, Bd. 2.

nucleus. The spermatozoa are made up into packets or spermatophores in the vas deferens.

Female.—The ovary also consists of two long lobes extending forwards on each side of the stomach to the green gland, and backwards to the second segment of the abdomen. The two lobes are joined near the middle, and just posterior to the junction give off the delicate oviducts which open on the basal segment of the third pereiopod. Pairing takes place at the period of ecdysis of the female, and the ova then are immature. The spermatophores are retained in the spermatheca until the

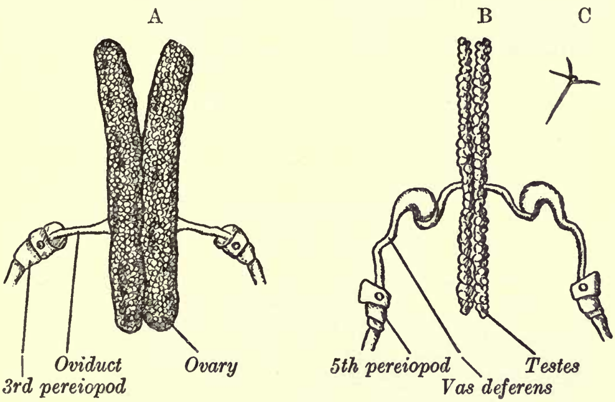


Fig. 52.—Nephrops. Reproductive organs: A, female; B, male; C, a spermatozoon greatly magnified.

ova are ready to be extruded. The latter are fertilised when they reach the brood chamber formed by the abdomen, and its appendages. The sperms are attached to the egg by the three neck processes, which contract, forcing the head into the ovum. The eggs are attached to the setae of the endopodites. The setae pierce the outer envelope of the egg, and the envelope forms a string of attachment. The fertilised ova measure 1·5 mm. in diameter.

Nephrops is liberated from the egg, after several months of embryonic life, as a larva with thirteen pairs of appendages, all but the abdominal appendages being formed. Such a larva is called a zoea. The pereiopods are furnished with the exopod, or swimming branch, and these are reduced to

vestiges and finally disappear when the young Nephrops begins its life on the bottom. During the larval period of weeks it is planktonic and drifts in the currents of the sea. It moults three times and the abdominal limbs are produced. The stages are similar to those of the lobster, Homarus.

The period at which the larva is liberated varies sometimes even in the same order of Crustacea. In the primitive

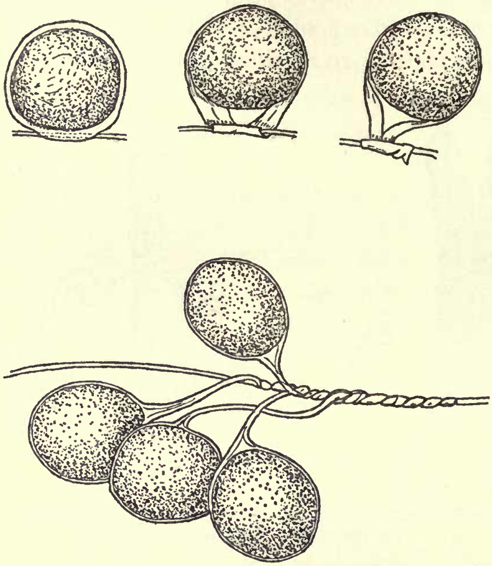


Fig. 53.—Carcinus. The attachment of the eggs to the setae of the pleopods. After Williamson.

fresh-water groups, as in some of the others, the larva possesses only the first three pairs of limbs, the two pairs of antennae, and the pair of mandibles. This is called the nauplius larva. The remaining limbs are added at successive ecdyses. Four kinds of larvae are commonly found, and according to the number of functional appendages these may be defined as: three appendages, ' nauplius '; more than three but not more than eight, ' protozoea '; eight but not more than thirteen, ' zoea '; all limbs present but not yet as adult, ' megalopa.'[1]

[1] *Report Cullercoats Laboratory*, 1918.

Ecdysis.—The periodical casting of the cuticle is of the greatest importance in the life of the Crustacean. During the instar material is accumulated, and this is brought into use when the shell is shed. Before ecdysis the cuticle is separated from the ectoderm and a gelatinous secretion invades the space. The cells of the ectoderm are enlarged, they contain glycogen, and they proceed to form a new cuticle. In the

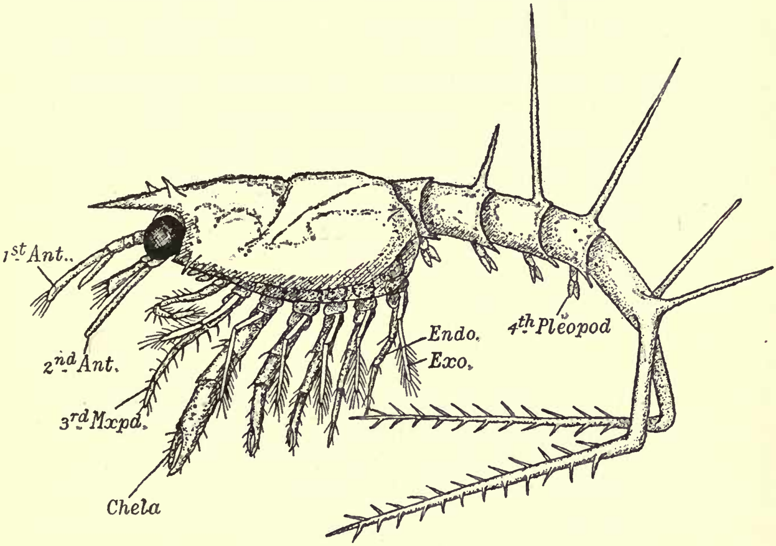


Fig. 54.—Larva of Nephrops.

case of larvae which are changing their morphological characters the new formation involves the new structures associated with the next larval stage. As has already been observed, the ecdysis consists in the shedding of the old cuticle and its internal prolongations. The back is raised, and pressure being brought to bear on the thin region between the carapace and the abdomen, this membranous part is burst, forming an opening through which the Crustacean emerges. The forward appendages are released, and the spines with which that region is furnished are brought to bear on the old cuticle in obtaining a purchase. Finally the rostrum reaches in this way the hinder margin of the carapace, and the spines of the

rostrum enable the creature to free entirely the forward part of the body from the old shell. When this is accomplished the tail is easily shaken off. The old cuticle is shed usually in the complete state and falls into its original form. After the ecdysis the new cuticle becomes hard and the ectodermal cells sink once more into a flattened state. The other tissues are also profoundly affected and only slowly recover. The blood at once gains in volume through the action of the digestive gland, and the result is that the new cuticle is distended to the new size. The lime salts accumulated in the digestive gland are liberated and undergo chemical change, to be used in the hardening of the cuticle. The muscular tissue takes a long time in recovering in the adult, when also the gonads are in an immature and reduced state.

The shedding of the cuticle produces a significant periodical loss, and the loss may be regarded as a special excretion. It serves the purpose also of freeing the crustacean from the varied life which obtains a lodgment on the cuticle.

CHAPTER VII

INSECTA

Phylum Trochozoa
Sub-Phylum Articulata
Division Arthropoda — *Types*
Class Insecta . . . Blatta
Anopheles
Culex
Glossina

The Insecta, or Hexapoda, excel all other classes in actual numbers, and the number of species is estimated to be about 45 per cent. of the total number of species of animals. Most insects are able to fly and, like the birds, their bodies are highly charged with air. The young state is spent in feeding and growing, usually in terrestrial conditions. Many spend this part of their lives in fresh water, and a few insects are found in or near the sea. Insects are usually small in size, but in the tropics large members of some of the orders are found. The body is divided into head, thorax, and abdomen. The thorax of three segments bears the characteristic three pairs of legs and typically two pairs of wings.

The life-history in many is through a metamorphosis familiar in the terms caterpillar, chrysalis, and winged or perfect insect. Larva is the name given to the caterpillar and the corresponding stage in other groups. A caterpillar is formed in the case of butterflies and sawflies, and the same stage of flies is called a maggot, and of beetles, grub. The chrysalis and corresponding stages are termed pupae. It is a resting stage in many, but the aquatic pupae of gnats and mosquitoes and others are able to move about. Such are distinguished

as nymphs. The imago is the perfect insect, and this stage is usually a short one in duration.

There may be several generations in a year, as in the case of many insects which are harmful to plants of the garden and the field ; typically the life-cycle is completed in a year, but may occupy two years, or three years as in the case of the beetles called in the larval state wireworms, four years in the case of the cockchafer beetles, and the American locust, *Cicada septendecim*, is said to live seventeen years. Only a few insects in the imago state survive the winter of the northern hemisphere. The plant lice, or aphides, reproduce parthenogenetically all the summer, males appear in autumn, and the fertilised winter egg remains in the unhatched state until spring, when it ushers in again the generations of parthenogenesis.

Blatta.—The common cockroach, *Blatta orientalis*, has been got in the wild condition only in the Crimea. Whether the Crimea is its original home is questionable, but it is now spread in kitchens and bakehouses in every part of the world. It appeared in Western Europe in the sixteenth century, and its spread has been produced by ship and land transport.

Another genus, Periplaneta, with the well-known species *P. americana*, is also common and cosmopolitan. It appears to have originated in South America. It is brought to this country by ships, and it is principally found in ships and at seaports. The genus is easily distinguished from Blatta by the greater size and by the large size of the wings, which are longer than the abdomen in both sexes. *P. australasiae* is a native of the East Indies, and is characterised by yellow bands around the antennae and on the first segment of the thorax and the elytra. This species has likewise become widely spread. For further information with regard to these and other species see Lucas (1920, ‘ Ray Soc. Monogr. of British Orthoptera ’).

External Characters.—The ectoderm secretes a chitinous cuticle resolved into the thick segments and the thin membranes between them. The cuticle is also secreted by the ectodermal invaginations of the alimentary canal and respiratory tubes. During the period of growth the cuticle is shed periodically, so

that, as in the lobsters, there are instar periods separated by ecdyses.

The head is flexed below the thorax, and, like the body, it is flattened. Laterally the surface is occupied by the large compound eyes. Between them the surface is divided into the epicranium and the clypeus, to which is hinged the front lip, or labrum, depending like a curtain in front of the mouth.

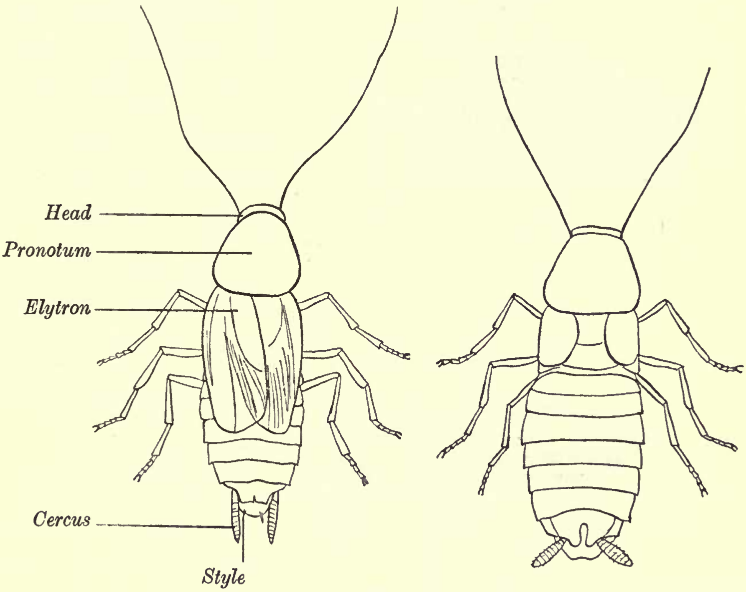


FIG. 55.—Blatta. Male (left) and female (right).

Two pale spots on the epicranium, close to the antennae and at the ends of the forks of the epicranial suture, are called fenestrae, and are replaced in the males of some species by ocelli, or simple eyes.

The appendages of the head are as follows. The pair of antennae are long and jointed, and in function they are tactile and olfactory. The mouth appendages lie behind the labrum. The mandibles are strong, flattened plates, and each is toothed at the inferior inner border. The first pair of maxillae consist each of a basal protopodite of two segments, termed the cardo and the stipes; of an endopodite borne by the stipes, the two

elements of which are called the lacinia (inner) and the galea (outer); and of an exopodite of five segments forming the palp. The second pair of maxillae are fused together basally to form the posterior or lower lip, the labium, of the mouth. The fused protopodites consist of the submentum and the mentum, and the latter bears the endopodite, which is divided into the ligula or lacinia (inner) and the paraglossa (outer) and an exopodite of three segments, the palp. On the floor of the mouth a chitinous structure is present, termed the lingua, or hypopharynx.

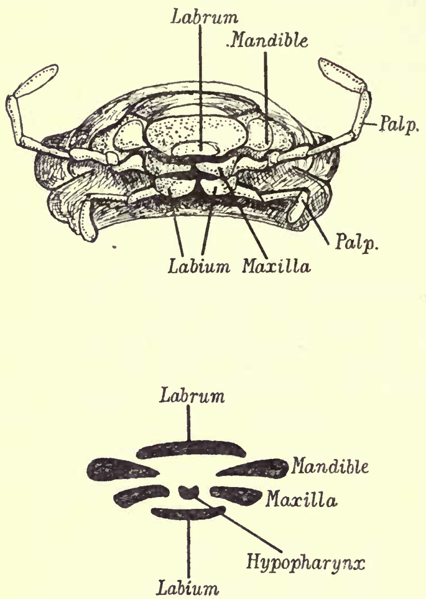


FIG. 56.—Blatta. The upper figure shows the mouth parts in position. The lower figure is a plan of the mouth parts.

The neck is narrow and tubular, and its cuticle is thin except in six small patches, which are termed sclerites.

The thorax consists of three rings, or segments, with intervening thin connexions. The dorsal part of the ring in each is called the tergum or notum, and the ventral the sternum. The pronotum is very large, forming the prominent anterior segment of the body. The mesonotum and the metanotum are about equal in size. The legs are borne by these segments, one pair on each. The legs are jointed, the segments varying in length. In Blatta and its allies the proximal segment, the coxa, is characteristically large, and the tibia is armed with spiny outgrowths. The segments in succession are named coxa, trochanter, femur, tibia, and terminally there is a six-jointed tarsus, the last of which bears the two claws (fig. 58).

The wings are borne on the last two segments of the thorax. The first pair are thickened to form a protection to the membranous hinder pair, and are called elytra. In the male the elytra reach to the fifth abdominal segment. The posterior pair are thin and membranous, and are the organs of flight on

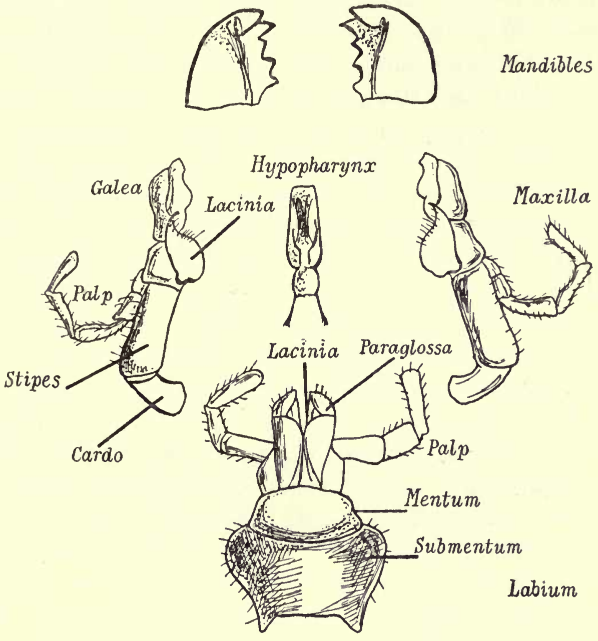


FIG. 57.—Blatta. Mouth parts in detail.
NOTE.—The lacinia of the labium is often termed the ligula.

the rare occasions when flight is resorted to by the males. In the female, both the elytra and the wings are rudimentary.

The segments of the abdomen number ten, and each is resolved into a tergum and a sternum. The anal opening is terminal, and the genital opening is ventral to it. A pair of podical plates situated one on each side of the anus is believed to represent an eleventh segment. In both sexes the first segment is small, but sex produces differences with regard to the posterior segments. In the male the eighth and ninth segments are apparent, but in the female they are telescoped

below the seventh, the ventral plate of which is enlarged to form the lamina subgenitalis. This is the terminal ventral plate of the female. In the male the terminal ventral plate is the ninth, and it bears a pair of styles. The shape of the tenth tergum is different in the two sexes, and it bears in both the segmented appendages called cerci. The purpose of the cerci is not understood. They are evidently homologous to the forceps of the nearly allied earwigs, and are believed to function as posterior tactile, perhaps olfactory, organs.

The openings are the mouth, anus, and genital apertures. In addition there are ten pairs of spiracles or stigmata, which open into the tracheal respiratory system: eight on the first eight abdominal segments, and two on the thorax. On the thorax they are situated between the legs on each side and between the first and second and the second and third segments.

Internal Structure.—Movement is produced by striated muscles attached to the segments as in the lobster.

The **alimentary canal** consists of a fore-gut or stomodeum derived from ectoderm; a mid-gut or enteron of endoderm; and a long hind-gut or proctodeum formed, like the stomodeum, of ectoderm. Both the stomodeum and the proctodeum are lined by chitin. The mouth is armed by the appendages already described. The food is placed in the mouth by their action, and in the cavity of the mouth it comes under the influence of the fluid poured out by the salivary glands. There are two salivary glands and a salivary receptacle on each side of the crop. The long ducts of the two salivary glands join to form a single duct which gives off the duct leading to the receptacle. The salivary ducts thus formed on each side fuse to make a common duct, and this opens on the hypopharynx of the posterior side (floor) of the mouth cavity. The short oesophagus expands into the crop, a wide and large portion of the alimentary canal in which the food is stored. It narrows rapidly at its hinder end to open into the small thick-walled gizzard, or proventriculus, which is provided internally with chitinous teeth and posteriorly with setae. The food undergoes a preliminary digestion in the crop, and is introduced as required into the gizzard, where it is masticated

by the teeth and strained by the setae before being introduced into the enteron.

The enteron, or chylific ventricle, is the region where digestion is completed, and where absorption of the food takes place. It is like the intestine which follows it, but is marked in front by the club-shaped digestive glands, and it ends just in front of the filamentous Malpighian tubules. The opening of the gizzard projects into the anterior end of the enteron, and it is here that the food receives the digestive fluids containing enzymes from the tubes of the digestive gland. These

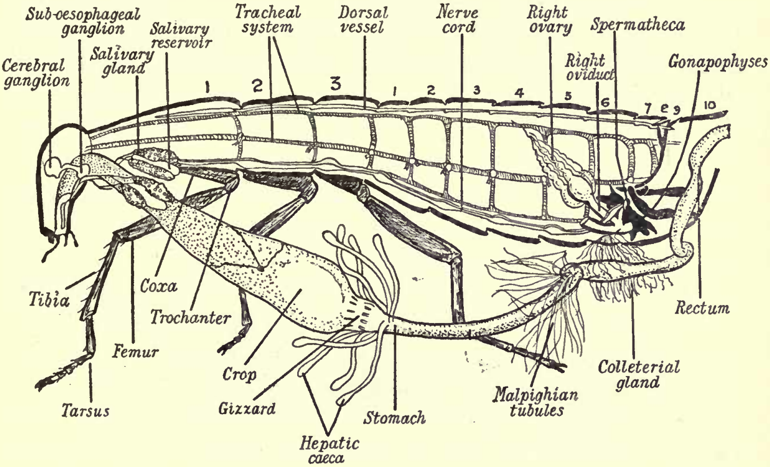


FIG. 58.—Blatta. Diagram illustrating the general anatomical structure of a female. The thoracic and the abdominal terga are numbered.

act upon the food and resolve the soluble part into a solution containing peptones, sugars, salts, and an emulsion of fats. These are absorbed by the endoderm cells and passed into the blood. The residue is carried along the intestine to be discharged or egested.

The proctodeum, or intestine, is marked at its origin by the Malpighian tubules, and its forward part has been called the ileum, the middle the colon, and the terminal wider part the rectum.

Respiratory Organs.—Respiration takes place by tubular invaginations of the skin called tracheae, and their openings

to the exterior, spiracles. The spiracles are provided with valves which render the opening crescentic. In most insects the spiracles are protected by setae from the ingress of dust. The ten spiracles of the cockroach lead into tubes which anastomose at once to form on each side a long lateral tube. From these other tubes emerge which divide, part going dorsally and part ventrally, and splitting up into innumerable branches which ultimately end blindly in every part of the body. The tracheae are lined by a chitinous cuticle strengthened by a fine spiral thickening, but their ultimate branches, the tracheoles, have no such lining. The air is thus carried to all the organs and tissues, respiratory gases being exchanged at the tracheoles, and the blood is therefore relieved of the office of carrying the oxygen from a respiratory organ to the distant parts of the body. The air contents of the tracheae are renewed by respiratory movements. The contraction of the muscles of the abdomen expels the air, and inspiration takes place with their relaxation. The action may be seen in the case of bees on the alighting board of a hive.

Circulatory System.—The blood is colourless and is provided with leucocytes. It is spread in undefined spaces all over the body and appendages. The blood is circulated by a heart, which with the anterior aorta are the only vessels. The heart is a long vessel extending under the dorsal skin of the thorax and abdomen. It is provided with thirteen pairs of ostia opening into as many chambers of the heart. Each ostium is provided with valves. The blood is forced out of the heart anteriorly into a vessel directly continuous with it, and this vessel, the anterior aorta, opens at once into the cavity of the head. The action of the heart in removing the blood around it draws a further supply into the pericardial space, which is somewhat defined from the rest of the blood spaces of the body by a septum, and the blood of the body is thus attracted to flow towards the pericardial sinus. During its circulation it obtains food absorbed from the enteron, which it conveys to the cells throughout the body, and it obtains from them the waste material from which it is relieved by the Malpighian tubules.

Nervous System.—The brain, or cerebral ganglion, is highly developed in the cockroach, as it is in insects in general. It

occupies the region of the head between the oesophagus and the epicranial wall, and it is supported on a chitinous ingrowth, the tentorium. The two large fused ganglia of the brain are produced into optic and antennary lobes on each side, and these supply the nerves to the eyes and the antennae respectively. Circum-oesophageal commissures connect the brain with the sub-oesophageal ganglia, which are also fused and supply nerves to the mouth appendages. These ganglia are the first of the ventral chain of ganglia, which is made up besides of the three thoracic ganglia, one to each segment of the thorax, and the six abdominal ganglia situated in the first six segments of the abdomen. The last of the series supplies nerves to its own and all the remaining segments. The successive pairs of ganglia are connected by double commissures.

A visceral nervous system arises from the circum-oesophageal commissure as a pair of nerves which unite above the oesophagus in a ganglion, and, running backwards over the crop, the nerve is joined by a pair of nerves issuing from the brain. The course of these nerves is easily followed on the crop.

The nervous system in insects is in a highly developed condition, and associated therewith the nervous activities are of a high order and have often been discussed by the naturalist and by the student of animal behaviour. The nerves are spread to all parts of the body and ramify in particular in the skin. They thus bring into intimate association all parts of the body. It has been shown also that the ventral ganglia are capable of inducing automatic movements apart from the brain.

Special sense organs are developed : the antennae, which are tactile and olfactory ; the eyes ; the cerci, which appear to function as posterior tactile organs, and tactile cells with setae throughout the skin.

The eyes are like those of the lobster, and consist of a large number of closely adpressed hexagonal facets, or ommas, derived from the ectoderm, separated by upper and basal masses of pigment. Each consists of a transparent cornea and crystalline cone, a long rhabdome surrounded by the retinula, and the

latter is continued through the basal membrane as the nerve (see p. 106).

Excretory Organs.—The excretory organs are the Malpighian tubules, which in the form of a large number of fine tubules encircle the anterior end of the proctodeum, and project into the haemocoel surrounding the gut. They take up the excretory products gathered by the blood, and the excretion is discharged through the intestine. The fat body also takes part in excretion (see below).

Body Cavity.—It has been plain from the foregoing account that the cavity of the body is a primary body cavity and almost completely a haemocoel. The blood bathes all parts of the space between skin and alimentary canal, and this space is crossed by the numerous tubes of the respiratory organ, and the walls of the cavity are occupied by nerves which, like the tracheae, have a universal distribution in the body and appendages. The haemocoel contains a loose connective tissue, especially around the abdominal viscera, and its cells are distended by fat. This is the tissue called the fat body, and appears to be derived from the coelom mesoderm. It is largely developed in insects generally, and is very conspicuous. It is regarded as a reserve of food material, and appears also to take a share in excretion. The coelom is therefore practically non-existent. It is represented merely by the gonocoel in each sex, and the ducts of these are coelomiducts.

Reproductive Organs. Male.—There is a pair of testes, difficult to isolate from the fat body. Each testis opens into a fine vas deferens, and the two vasa open into the mushroom-shaped seminal vesicle. From the seminal vesicle the ejaculatory duct leads to the external aperture below the anus. The aperture is surrounded by plates and processes, called gonopophyses, and with these are associated the styles.

Female.—The ovaries consist on each side of eight tubes in which the developing ova are plainly visible. The tubes unite posteriorly to form the oviduct, and the two oviducts unite to open by a single vertical aperture to the exterior. Between the opening and the anus are strong chitinous processes, the gonopophyses. Accessory to the female organs are the spermathecae, two sacs which open on the ninth segment,

and in which the sperms are received from the male and stored; also the colleterial glands, a pair of highly developed branched glands opening separately just behind the aperture of the spermathecae. The secretion of the colleterial glands forms the capsule for the eggs.

It is evident that in pairing the spermatic fluid is transferred by the male to the spermathecal pouches of the female, and that, as in the crustacean, the act of fertilisation may take place long after the event of pairing. The eggs are fertilised when they are ripened and liberated. The sixteen eggs freed from the sixteen tubes of the ovaries are held by the gonopophyses until the secretion of the colleterial glands has been completed around them into an egg-case, 'cocoon,' or ootheca, which contains the eggs and the spermatozoa.

The **development** of the egg is somewhat complicated. A general blastoderm is produced, the yolk not segmenting, and the blastoderm surrounds the egg. The cells are flat dorsally, but ventrally are columnar. The posterior cells, followed by the anterior flattened cells, are produced into folds which meet and fuse to form an amnion over the ventral thickened part of the blastoderm. A long median groove is formed on this ventral embryonic portion, and from this is derived the endoderm and the mesoderm. The endoderm subsequently encloses the yolk, the mesoderm is resolved into a series of coelomic pouches, and an anterior stomodeal and a posterior proctodeal invagination appear and deepen, to meet and fuse with the enteron. The growth is accompanied by changes which vary according to the group, and in some cases are profound; but in all the coelom becomes practically obliterated by the overgrowth of the mesenchyme and the haemocoel, and persists only in the formation of the gonadial tubes. The tracheae are developed by ectodermal invagination, and the wings and limbs as expansions of the body wall.

The young cockroach at hatching is white in appearance, but the eyes are black. It is in all respects like the adult except in size and the absence of wings. Some five to seven ecdyses are passed through, and at the last ecdysis it is furnished with wings in the male or their rudiments in the female.

Insects exhibit a great deal of variation from the structures illustrated by the study of such a type as the cockroach, but the essential features are not departed from. The modifications mainly affect the mouth parts, the wings, and the proportional development of the regions of the body and the stages of development. While a perfect system of classification is still a desideratum, the following orders, based on the condition of the wings, may be recognised. Thus, obvious modifications allow of classifying the two-winged insects or flies as Diptera, the scale-winged butterflies and moths as Lepidoptera, the membrane-winged bees, wasps and ants as Hymenoptera, the sheath-winged beetles as Coleoptera, the straight-winged cockroach, earwig, leaf insect, locust, cricket, and grasshopper as Orthoptera. Some members of the groups mentioned are wingless, but other characters serve to show their relationship, and there are groups which are characteristically without wings. Such are assumed to fall into Apterygota, which never have been winged, and Anapterygota, which have secondarily become wingless. But the assumption is open to question, and the classification is artificial and imperfect.

The wingless groups have a simple development, the young being hatched with a form similar to that of the adult. The Orthoptera and one or two other groups differ only in that wings are produced. The large majority pass through the stages already mentioned, and the successive phases of life are sharply marked by morphological peculiarities.

Insects are economically important in various ways. Several species are useful, as the bee, the cochineal insect, and silk moth; many serve a useful purpose in the fertilisation of flowers; and certain others, as the hymenopterous Ichneumons and the dipterous hover flies, the Syrphidae, destroy harmful insects.

Insects and Diseases.—But it is in their relationship to disease that insects have in recent years been found to play an important part. Before that period they were known as parasites, from which man was not exempt, and they may under circumstances be developed in such numbers as to be a danger to crops in the field and in the nursery, and to produce in granaries and warehouses.

Two groups of flies have been found to be the means of communicating tropical diseases, as malaria and sleeping sickness.

Malaria.—The family Culicidae of Diptera, the gnats or mosquitoes, consists of some 1000 species, and a section of the family containing about 100 species is the Anopheline group, important from their rôle in the transmission of malaria.

The eggs of the mosquito are laid by the female on the surface of water of ponds, canals, streams and the like. The egg is flattened and boat-shaped, provided at the sides with

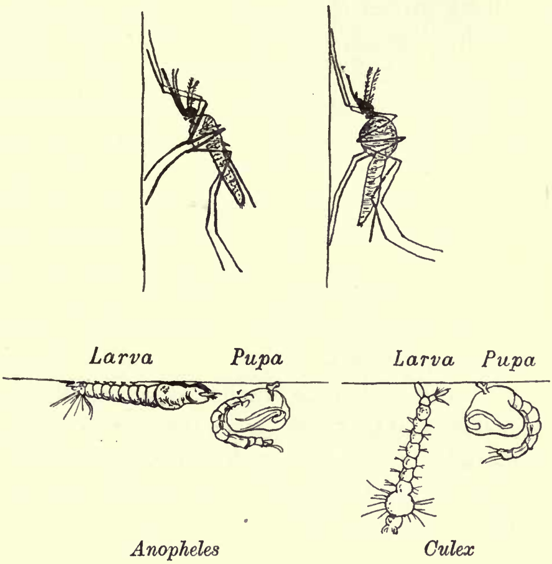


Fig. 59.—Diagram to illustrate the life-histories of anopheline and culicine mosquitoes. The larvae and the adults are shown in the resting position.

ribbed floats, and is laid singly in the case of the Anophelines, in rafts in that of the Culicines. In about two to four days the egg of the former liberates an active larva. The larva is resolved into head, thorax, and abdomen. The head possesses small lateral eyes, short antennae, and strong mandibles and maxillae. The segments of the thorax are broad and fused. The abdomen is of nine segments ; the eighth segment bears the stigmata or spiracles, the two openings surrounded by a shield. There is no siphon as in the larva of their near allies the culicine mosquitoes. The presence or absence of the siphon makes

it easy to distinguish the larvae of anopheline and culicine mosquitoes. The anal opening is terminal and surrounded by four papillae.

On account of the absence of a siphon the larva lies immediately underneath and parallel to the surface of the water. In this position it feeds greedily and changes its position by backward jerking movements, and when disturbed it sinks to the bottom.

During its growth the larva sheds its cuticle several times, and when fully grown it changes at once into the comma-shaped nymph or pupa. In this state it does not eat, but nevertheless it is capable of movement under certain conditions. The pupa breathes by short funnel-shaped spiracles situated dorsally on the thorax. This is also the case in the culicines, but in them the spiracles are produced into long slender tubes. After several days of nymph life the imago, or adult insect, is produced from the pupa by exuviation and begins its aerial life. It is very different from the preceding stages. The body is elongated, the legs attenuated, the thorax bears the membranous fore-wings and the rudimentary hind-wings, called halteres.

The head bears antennae, highly setate in the male, and large eyes. The mouth appendages, which reach their highest development in the female, consist of piercing and suctorial organs and a sheathing organ. The former are designated labrum-epipharynx, mandibles, maxillae (first pair with their palps), and the hypopharynx. The sheathing organ is the labium (the fused second pair of maxillae). In attacking the host for the meal of blood the piercing organs inflict the wound, the hypopharynx carries a stream of saliva into the lesion, and the blood is drawn up the tube formed by the apposed labrum-epipharynx and the hypopharynx. The current of blood is induced by the pumping pharynx, which is the anterior portion of the alimentary canal. The labium, except to guide the stabbers by its tip, takes no part in the process, its chief function being to sheath the stylets when at rest. The male, which is a vegetarian feeder, lacks mandibles, while the maxillae are not so strongly developed and the hypopharynx fuses with the labium.

The middle element of the thorax is the largest. The nervature of the wings is utilised in insect classification and is employed in this group to distinguish the species. Eight segments are visible in the abdomen, and the openings are terminal. The females only suck blood, and it is through them that malaria is communicated (p. 25).

Malaria is communicated by species of various genera—Anopheles, Cellia, Myzomyia, Myzorhynchus, Nyssorhynchus, Pyretophorus. Anopheles was once common in England, and three species may still be found. The adults tend to be common where the conditions of water, and habitation of man, or of mammals and birds, occur together.

Another dipterous genus, Glossina, tsetse flies, has become important from the fact that it is the means of introducing the protozoan parasite

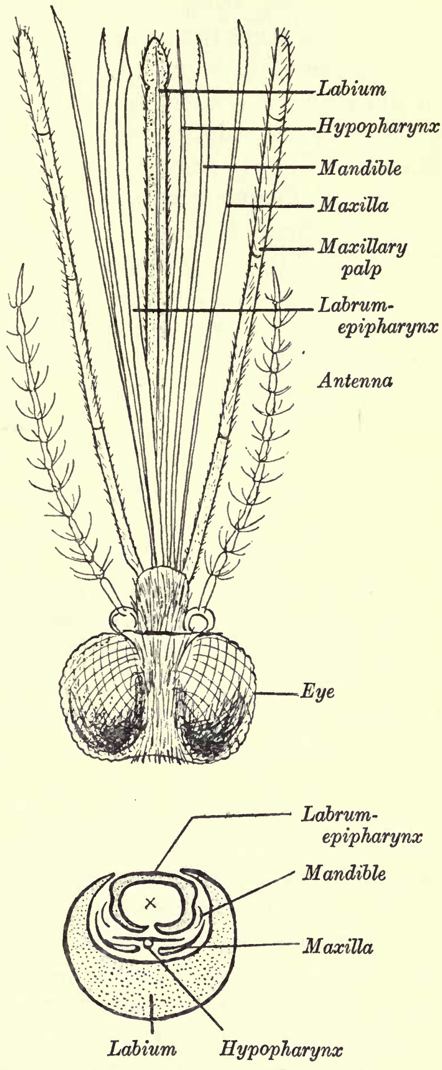


FIG. 60.—Anopheles. Head appendages of female, spread out and viewed from the dorsal aspect. The transverse section of the mouth parts (after Nuttall and Shipley) should be compared with fig. 56.

of sleeping sickness to man, and it is also concerned in certain animal diseases [1] (see page 28).

Insects are to be distinguished from the eight-legged spiders, mites and ticks which belong to the Arachnida. Ticks may also serve to communicate disease, as Texas Cattle Fever in America and Louping-ill to sheep in Britain.

The study of insects has therefore become an important branch of Zoology relating to agriculture and to medicine.

General Considerations.—A few remarks may now be made as to the main features of the preceding metazoon groups. The Coelenterates are diblastic, and the two layers, the ectoderm and the endoderm, are related, as in the gastrula stage of development of the other groups. The Platyhelmia are provided with a mesoderm interposed between the two primary layers, and it is resolved into a gonocoel and mesenchyme and muscles. The mesoderm is invaded by ectodermal invaginations which branch in the spaces among the mesenchyme cells and end in flame cells or solenocytes. These primitive kidneys are called protonephridia. The Rotifera are very similar in constitution, but the space is large and distended by a fluid, and the gonocoel projects into it from a pouch at the posterior end of the alimentary canal. The mesenchyme spaces have been converted into a primary body cavity or schizocoel. The gonocoel is endodermal in origin. The schizocoel possesses protonephridia of a nature and development quite similar to those of the Platyhelmia. With the exception of the gonocoel, the structure of the rotifer is that of the embryo or the larva of the other Trochozoa. The remaining Trochozoa have the mesoderm of the post-embryo or post-larva and adult resolved into two distinct spaces: (1) the primary body cavity, homologous with the primary spaces into which the blood penetrates; (2) the secondary body cavity or coelom, homologous with the gonocoel, for it has a similar origin and primarily the same function.

With relation to the primary body cavity, protonephridia are developed from the ectoderm and function throughout life not only in the Rotifers but in lowly groups allied to the

[1] 1913, Castellani and Chalmers, *Manual of Tropical Medicine*; 1911, James and Liston, *A Monograph of the Anopheline Mosquitos of India.*

Mollusca and the Annelids, in endoproct Bryozoa, and also, as we shall find, in the vertebrate Amphioxus. They are developed as temporary organs of excretion in many Mollusca, and in land and aquatic Annelida. They are also formed in larval Sipunculidea, Brachiopoda, and Phoronidea, and in these they are converted by forming an opening into the coelom into an organ which, continuing its function of excretion, assumes that of a gonoduct. The growth of the Annelid and its characteristic meristic segmentation have led to a series of protonephridia being formed. The anterior ones are suppressed—that is, after the embryonic or larval phase, during which they are associated with the primary body cavity, or head cavity, as it is sometimes called. The posterior ones, developed in succession in regular order from the ectoderm, are put into communication with the coelom and are nephridia. In some cases they may act as gonoducts.

The larval nephridia of Mollusca are altogether absorbed, and the coelom develops another kind of duct, as an outgrowth from the coelom—that is, it has a mesodermal origin and gains an opening through the body wall. It recalls, and may be said to be homologous to, the terminal ducts of the gonocoel of the Platyhelmia. The coelomiduct acts as a gonoduct in Annelida, and in the Polychaeta in certain cases it may be conjoined to a nephridium.

The coelom of the Arthropods undergoes great reduction. It may be that the tough cuticle of the Arthropods has made it unnecessary to have a watery distension of the body, such as the coelom provides in their softer-skinned allies. The result has been that no nephridia are formed, and such ducts as are produced in relation to the gonads and the kidneys of Crustacea are coelomiducts.

The Metazoa illustrated by the preceding examples are characterised by a fundamental feature of development. The blastopore is carried in to form the mouth, or, if it be closed, it marks the place where the mouth will arise. For this reason this section of the Metazoa could be linked together as Stomoporida. The polarity is seen in the Coelenterata, where the anterior end is the fixed end, and the posterior end that from which the tentacles are produced and at which the mouth

opening is formed. In the succeeding phyla the blastopore is rotated forwards, but it still forms the mouth. It is only in some of the Arthropods that the blastopore elongates so as to give rise to the anus as well, but even so the mouth is still formed from the blastopore. The mesoderm is at first derived from both ectoderm and endoderm, but in the Stomoporida the mesoderm becomes more strictly related to the endoderm; and in some of the Platyhelmia, the Rotifera, the Annelids and Mollusca, investigations have been able to show that certain of the cells produced during segmentation form the ectoderm and its products, others the endoderm, and a special cell the mesoderm. The latter is invaginated with the endoderm. This relationship of the mesoderm to the lip of the blastopore or to the invaginated endoderm is maintained in the remaining groups.

The blastopore of the remaining phyla is directly related to the formation of the anus, and the mouth is formed independently of it. These phyla may therefore be brought together as Proctoporida. The Invertebrate representatives may be grouped under the name Hydrocoela, and include the Chaetognatha or arrow worms, Echinoderma or starfishes, Pterobranchia and Enteropneusta.

Endocrinology.—Morphology is a fascinating study, but we must not forget that the animal is still more interesting alive, that the structures we expose by dissection and examine in detail with the aid of the microscope are the structures which make a living creature and by which it is kept alive. We have had time to think of this to some extent, but the exigencies of time and opportunity necessarily make our laboratory work an enquiry mainly into structure.

Every cell, whether it be free or a component of a cell complex, is related to its environment, and the reactions of the ectoplasm to the environment are conveyed by chemical and mechanical changes to the endoplasm by the cell sap. The intercellular sap, as we may term the fluid which circulates among the mesenchyme cells of the primitive metazoon, similarly communicates the effects of the environment to the whole body, and mechanically as well as chemically, for the pressure it exerts by virtue of its condition with respect to food will

serve to act and react throughout the body. The cells of the metazoon are not merely related by nerves which bring them under a central influence, but by a still more primitive means of communication by chemical suggestions conveyed from one organ to another, or to the body as a whole, and so potent that, rather than having been replaced by a nervous system, the system has been perfected. This function is taken over by the blood, which is the direct descendant of the mesenchyme. The blood is not only a carrier of food, of oxygen, and of waste material, it is the ever-circulating path along which chemical impulses are conveyed. The impulses are related to environment, to growth, and to reproduction. The effects are made known by definite movements resulting and by changes in growth. Such impulses have proved so useful to the animal that special organs have been developed to produce by secretion the chemical agents which are distributed by the blood. Such organs are called endocrine organs ; and the internal secretions to which they give rise, endocrines or hormones. But they are special manifestations of a system which concerns and serves to relate the body generally.

CHAPTER VIII

CEPHALOCHORDA

Phylum Vertebrata
 Sub-Phylum Acraniata
  Class Urochorda — *Type*
   Cephalochorda . . Amphioxus

The Acraniates include the Ascidians, and Amphioxus and Epigonichthys, which two genera constitute the Cephalochorda. Both classes are marine, and are related to the Hydrocoela, which are also marine. Amphioxus presents lowly vertebrate features, features which are passed through in the development of the craniates, in addition to others which are incorporated in association with its lowly vertebrate structure and its manner of life.

Amphioxus lanceolatus is common in shallow water in certain regions in the Adriatic, at Messina, Naples, and other parts of the Mediterranean, in the western region of the English Channel, in the Heligoland Bight, in the Cattegat, and it has been observed at various places on the west coast of Norway up to Trondhjem. It was obtained during a Government survey in 1921 on the Dogger Bank. It occurs on the Atlantic coast of America and has been recorded from Ceylon. Other species are found in tropical and temperate seas generally, so that the genus is world-wide in distribution, and the species are very similar in structure.

External Morphology.—*Amphioxus lanceolatus* is small; it measures scarcely two inches long when fully grown. In the living state it is transparent and has a fleshy tint. It burrows in sand and comes to rest in an upright position with the mouth

protruding. It feeds on suspended matter, mostly diatoms and minute animal life. At night it becomes more active, and then has been observed to emerge from the burrow and swim about.

It has a symmetrical fish-like shape, tapering at both ends. The sides of the body are occupied by the <-shaped myotomes or muscle segments; the angle of the < is directed anteriorly. The numbers of the myotomes between the head and the atriopore and between the head and the anus are employed to distinguish species. In the lanceolatus group the preatrioporal myotomes number about thirty-six, and the preanal fifty to fifty-six. The species found on the west coast of America and at the Cape have myotomes which number respectively about forty-five and sixty.

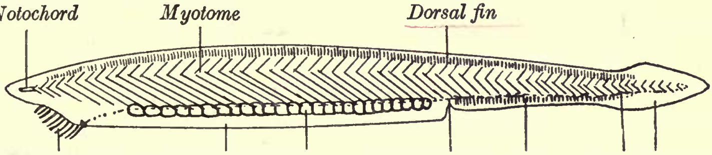


FIG. 61.—Amphioxus. The adult from the left side.

The body is laterally compressed, and the margin is produced to form a median fin. The dorsal fin runs from end to end of the body, and is expanded at the posterior end to form a caudal fin; and below, the median fin sinks again to form the ventral fin, which reaches forwards to the atriopore. Between the atriopore and the oral cavity paired folds of the body wall occur, subtending a ventral groove. These are termed metapleural folds. Between them and the myotomes are square-shaped masses which are the gonads.

Below the anterior extremity is the wide opening of the oral cavity. The cavity narrows internally to an opening which is the true, or at all events the original, mouth. The margin of the oral cavity is produced into numerous processes which are called cirri. The anal opening is on the left side of the ventral fin. The atriopore is the median opening at the posterior end of the metapleure and in front of the ventral fin; it discharges the contents of the atrial cavity.

Sections will show that the ectoderm is a single layer of columnar cells which secretes a cuticle externally and is based on a thin layer of connective tissue or dermis internally.

Internal Morphology.—The main features of structure can be made out by dissection, but it is better to examine prepared specimens of young and sections of the adult.

The **connective tissue** which forms a thin dermis under the ectoderm is continued into septa between the myotomes, and these internally are continued in the sheaths which surround the nerve cord and the notochord, and with fasciae which separate the muscles from the cavities below. The connective tissue also supports the median fins ; it is disposed in the form of a series of compartments filled with a gelatinous fluid, by means of which the fins are kept distended. The connective tissue, in short, is spread throughout the body, and it is continued from the one region and purpose to the next.

The **myotomes** are made up of horizontal muscle fibres, and these are striated. Each fibre is enclosed in a delicate connective-tissue investment, and the fibres pass from septum to septum in succession all along the body. They thus form a series of muscles on each side, extending from above the mouth to the end of the tail. It will be observed also that the myotomes of one side alternate in position with those of the other. The body-cavity region is long and the tail region short, and the presence of the myotomes so far forward allows of lateral movements throughout the whole length of the body, movements employed in swimming and in burrowing, and an Amphioxus may penetrate the sand either forwards or backwards. The myotomes are retained in a simple, unchanged state in Amphioxus. In the Craniata they are more or less fused and modified to form special muscles related to special actions, but all Craniates pass through a stage similar to that of the adult Amphioxus. In Amphioxus, however, the floor of the atrial cavity is provided with a sheet of transverse muscles, the function of which is to compress the atrial cavity and thus help in expelling the water.

The **notochord,** the essential characteristic feature of the vertebrate, is present also in Amphioxus. It extends from end to end of the body. It lies just above the central line

anteriorly, and posteriorly it is central in position. It is made up of cells which have become highly vacuolated, and the spaces are filled with a gelatinous fluid. It is surrounded by a tough connective-tissue sheath. The large vacuoles of the notochord are maintained in life in a turgid state, and the sheath provides an external resistance. It thus forms a central elastic skeleton which gives rigidity to the body, and it is bent by the action of the muscles on each side.

The **alimentary canal** is modified for the capture, digestion, and absorption of food, and for respiration. The oral cavity has a wide margin produced into cirri. The margin is kept distended by a skeleton of gelatinous bars which are produced into each cirrus. The cavity gradually narrows to the mouth opening, bounded by the velum. The oral cavity in front of the mouth or velum is raised into ciliated folds which form what has been called the wheel organ. The wheel organ is interrupted on the roof of the oral cavity by a pit, called Hatschek's pit, or the preoral pit. The velar margin is produced into a series of processes which are called velar tentacles. These structures are best seen in prepared specimens of young Amphioxus and in sections.

The functions of these organs are not very apparent. Hatschek's pit appears to be a mucin-secreting gland, and may thus serve to begin the process of providing mucin for entangling the food. It is possible also that, situated as it is on the roof of the oral cavity, it acts as an environmental organ—an organ, that is to say, designed to give warnings by internal secretions of changes in temperature and other features of the water. The cilia of the wheel organ and of the velar tentacles maintain and direct a current carrying food into the pharynx.

Beyond the velum the canal suddenly expands into the large pharynx. The pharynx occupies the whole of the metapleural part of the body; it is compressed laterally, but vertically it extends from near the notochord to the ventral region of the atrial cavity. At the anterior end the walls of the pharynx present a pair of ciliated bands, the peripharyngeal bands, which encircle the wall in an oblique direction and merge dorsally and ventrally in glandular grooves. The

lower—the hypopharyngeal groove, or endostyle—is a structure of great morphological interest, for it is developed in all vertebrates, and in the Craniata it is converted into the thyroid gland. In Amphioxus it is made up of elongated cells, some of which are glandular, some ciliated. The upper or epipharyngeal groove has a similar structure. Between these grooves, which are coextensive with the pharynx, the lateral walls of the pharynx are pierced by numerous gill slits. The gill slits are long narrow openings in the pharyngeal wall, extending obliquely from near the epipharyngeal to near the hypopharyngeal groove, and they open into the atrial cavity.

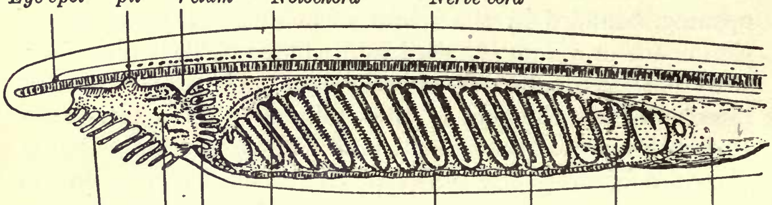


FIG. 62.—Amphioxus. The anterior end of a young specimen.

The atrial cavity is lined by ectoderm, so that the gills intervening between the slits are lined internally by a ciliated endoderm, and externally by ectoderm which is not ciliated. The slits are so numerous and the gills so narrow that the whole system has a very delicate structure. The gills are united by cross-pieces which split up the apertures into several apertures in each case. Moreover, in each gill a thin skeletal gelatinous bar is developed. The bars are connected above the gills, and they end ventrally below the gills, the ends being alternately single and double. The latter are called primary, and the former secondary bars. The regularity of the arrangement is due to the manner of development of the gills. The original slits of the young are divided by a downgrowth into two slits. The primary rods are forked ventrally, but the intervening secondary rods are not forked. Lastly, the pharynx is protected by the walls of the atrial cavity, which not merely

protect the delicate structures of the gill region, but allow of muscular contractions taking place in that region which occupies so large a share of the body.

The pharyngeal apparatus serves to filter off the food from the water, and as a respiratory organ. The cilia of the oral cavity bring about a constant current of water. There are no jaws, and the food in suspension is drawn into the pharynx. The endostylar glands secrete mucin which entangles the food, the cilia of the endostyle form the mucin into a rope, and this, with the aid of the peripharyngeal bands in front and the cilia of the gills over the rest of the pharynx, is gradually carried upwards to the epipharyngeal groove. The food is carried along the epipharyngeal groove to the posterior end of the pharynx, and so to the stomach.

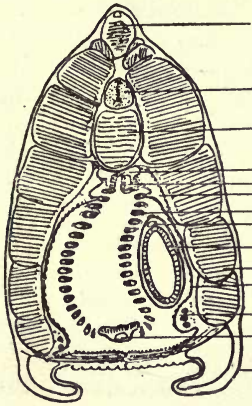


Fig. 63.—Amphioxus. Transverse section in region of pharynx.

The stomach is defined from the intestine only in being slightly wider and by its blind outgrowth on the right side. This is the liver, or hepatic caecum, the blind end of which is directed forwards on the right side of the pharynx. It carries with it a covering of ectoderm from the atrial wall. In the young it is short, but in the adult it reaches to the anterior end of the atrium. The epithelial cells of the caecum are columnar and glandular, and they are liable to be thrown off into the cavity and renewed. Digestion and absorption are performed in the caecum. As the cells contain granules, it is believed that the organ also takes a share in excretion.

The stomach, like the pharynx, is lined by ciliated cells, and these are continued into the intestine. The latter pursues a straight course to the anal opening, which, as has already been observed, occurs on the left side of the ventral fin.

Respiration is brought about by the gills removing oxygen from the water passing over them, and by the blood taking the oxygen up in exchange for such gaseous waste matter as can be dealt with by the gills. There is evidently no respiratory pigment, and the oxygen must therefore be simply dissolved in the plasma.

The **atrial cavity** ends blindly in front and opens posteriorly at the atriopore, beyond which it extends a short distance on the right side of the intestine. The water which is filtered through the gill slits is passed into the cavity and is discharged at the atriopore. In the young the gills open directly to the exterior, and the atrial cavity is developed by a median ventral infolding of the body wall.

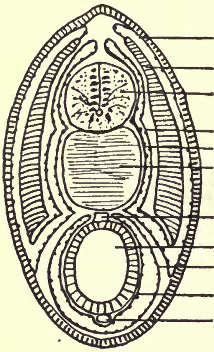


FIG. 64. — Amphioxus. Diagrammatic transverse section of abdominal region of larva.

A **coelom** is developed as a series of paired vesicles from the endoderm, and these are resolved into the somites, each of which contains a cavity called the myocoel, and into the body cavity, or splanchnocoel. The inner or visceral layer of the splanchnocoel enwraps the alimentary canal, and the parietal layer lines the body wall. This arrangement is preserved in the posterior region of the body, but in the region of the wall of the atrial cavity and the pharynx the cavity is divided into a series of tubes and spaces. Of these the coelomic spaces on each side of the dorsal region of the pharynx may be observed in sections, and the small canals of the coelom which traverse the gills from the endostyle to the dorsal coelomic spaces just mentioned. An independent space, the preoral cavity, occupies and distends the proboscis below the notochord. It is derived from the right head cavity of the larva, and the left one is reduced to form the inner part of Hatschek's pit, which opens on the roof of the mouth (see p. 149).

The rest of the mesoderm is relegated to the formation of the connective tissues and the blood system, and is but slightly developed.

Circulatory System.—The blood is a colourless fluid, or plasma, without corpuscles, which is circulated in vessels and sinuses, of which the heart and the aortae alone possess a wall. The disposition of the vessels, however, is of great interest. The heart is little more than an S-shaped bend of the vessel at the postero-ventral end of the pharynx. The blood is conducted forwards from the heart in a ventral aorta which lies below the endostyle. The ventral aorta gives off afferent branchial vessels which run up each gill, from which they emerge dorsally

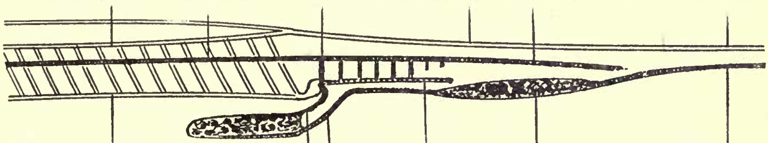


FIG. 65.—Amphioxus. Diagram of blood circulatory system.

as efferent branchials. The efferent branchials run into the dorsal aortae, paired vessels which convey the blood forwards to the head and posteriorly unite behind the pharynx to form a median dorsal aorta, and that in turn runs into the tail as the caudal artery.

The caudal vein returns the blood from the tail, and on entering the body from the tail splits into two vessels : (1) the subintestinal and (2) the right posterior cardinal veins. (1) The subintestinal vein forms a sinus system around the intestine. This plexus of the intestine gives off anteriorly a vein, the hepatic portal, which carries the blood to the hepatic caecum, around which it divides into a sinus system. The blood is collected from the hepatic sinuses by a hepatic vein which enters the right (the posterior) end of the heart. (2) The right posterior cardinal vein runs forwards from the caudal vein, and at the level of the heart it meets a similar vein from the right anterior side of the body, the anterior cardinal, and

at their junction a Cuvierian vein is formed which enters the heart posteriorly. Similar cardinal veins occur on the left side, and they form a left Cuvierian vein to connect them with the heart, but the left posterior cardinal does not reach the caudal vein. The Cuvierian veins, which are transverse veins, are paralleled by a series of transverse vessels posteriorly to them, the anterior of which enter paired vessels which bring the blood from parietal sinuses to the heart. The circulation is simple and primitive, but it is essentially that of the fish and of the embryos and larvae of the higher vertebrates.

The **central nervous system,** the dorsal nerve cord, extends from near the anterior end to near the end of the tail, and it is enclosed throughout in a neural canal formed of connective tissue. The anterior end is the brain, but it is not distinguished by size from the rest of the cord. Moreover, how much of the cord is brain and how much spinal cord cannot be said, for there is nothing to indicate where the one begins and the other ends. The blunt end presents a pigment spot, and after an interval pigment spots occur in the central canal all along the cord; the posterior end gradually tapers, as does the notochord below it. The front end of the cord is occupied by a cavity formed at the expense of the enclosing nervous wall, and the cavity is continuous with the central canal which runs throughout the rest of the cord. The anterior vesicle represents the forebrain of the Craniates, for it has an infundibular organ on the postero-ventral aspect of its floor. In the young the anterior ventricle of the brain is open to the exterior by the neuropore, but in the adult it is closed. The ectoderm leaves, however, at the spot a blind pit with an opening on the left side, and this pit has been called the olfactory pit. Below this is the pigment spot.

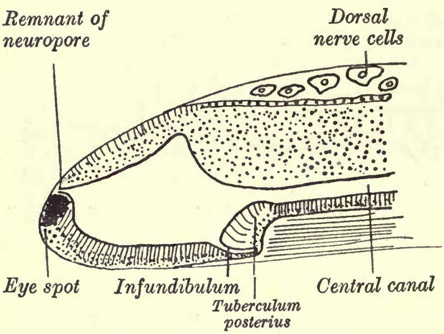


Fig. 66.—Amphioxus. Brain vesicle. After v. Kupffer.

The nerve cord is made up of nerve cells or neurons and their prolongations or axons, and these are supported by connective tissue. Some of the nerve cells are large and give off large axons, or giant fibres, which run along the cord. The smaller cells are mainly associated with axons which leave the cord in paired bundles, the nerves. Various writers have attempted to homologise the anterior nerves with the nerves of the Craniates. The nerves generally are segmental, and occur in an alternate series of independent dorsal and ventral roots. The dorsal arise singly from the cord, the ventral by a fan of separate fibres which supply the muscle fibres of the myotome opposite which each arises. The dorsal roots supply the skin and the transverse muscles of the metapleure. The dorsal roots are therefore like the dorsal roots of the brain of the Craniates in being intersegmental and extra-myotomic in distribution. The ventral roots agree in origin and distribution with the ventral roots of the brain and spinal cord of the Craniates. The dorsal roots are mixed—that is, they contain motor and sensory fibres—while the ventral are purely motor.

Anteriorly a pair of nerves arise from near the front end of the brain and are distributed to the proboscis; a second pair arise dorso-laterally and run to the pigment spot or eye spot. The mouth is supplied by a series of branches derived from the first eight dorsal roots.

The **excretory organs** consist of a series of protonephridia, and it is a remarkable feature of the creature's organisation. The protonephridia are ectodermal in origin, and are developed from the ectoderm of the atrial cavity as that cavity is being formed. They end blindly, and the epithelium of the tube is produced into numerous solenocytes which come into close relationship with the efferent branchials, against the walls of which the solenocytes impinge. They open dorsally into the atrial cavity, and there are about a hundred pairs altogether. They are interesting because they are so different from the kidneys of the higher vertebrates, because they are developed in the pharyngeal region alone, and because nephridia are not developed in the groups below to which Amphioxus is more nearly related (fig. 67).

Reproductive Organs.—The sexes are separate. The ovaries, as well as the testes, are about twenty-six pairs, developed from diverticula of the myocoels of the pharyngeal region. When ripe the products escape from the gonads, in each case by an opening formed specially, then into the atrial cavity. They are carried to the exterior by the atriopore, and fertilisation takes place externally.

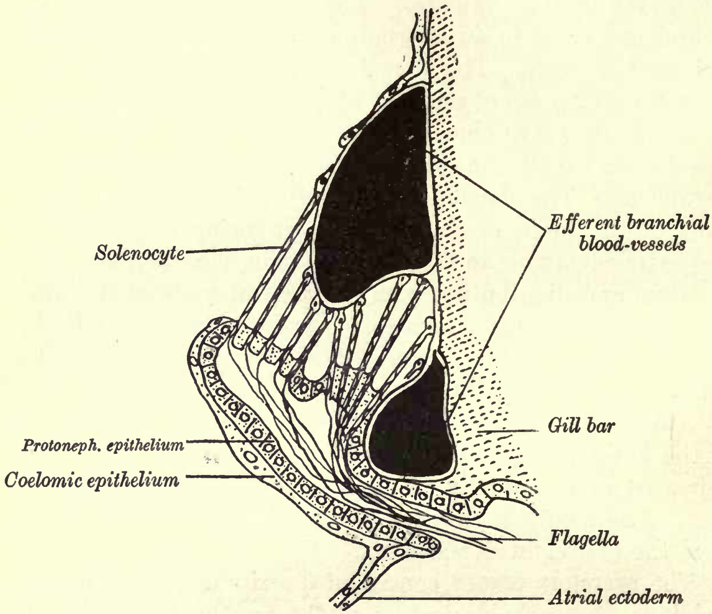


Fig. 67.—Amphioxus. Section of a protonephridium. After Goodrich.

Development.[1]—The eggs and the early and larval stages of development are planktonic. There is during the long period of at least three months a wide dispersion by passive drift or denatation. This is the reason that the adults are found in situations which are often widely separated. It has been proved, moreover, that the larvae may be transported across the ocean.

The ripe ovum of Amphioxus measures about 0·1 mm. It is covered by a fine structureless membrane, and the outer layer of protoplasm is differentiated to form an additional

[1] 1881. Hatschek, *Stud. u. Entwicklung des Amphioxus.*

inner protective envelope. The polar bodies extruded during the ripening of the egg mark the animal pole. Fertilisation takes place by the entrance of a spermatozoon, and the two nuclei fuse to form the segmentation nucleus. Segmentation is holoblastic and simple. Two furrows succeed one another

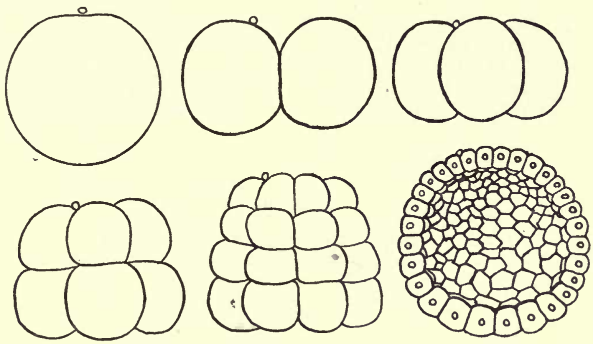


Fig. 68.—Amphioxus. Segmentation of egg with formation of blastula. After Hatschek.

through the polar field, and the four cells are converted into eight by a furrow at right angles to the first two and slightly nearer the animal than the vegetable pole. Segmentation proceeds regularly and yields a blastula of one layer of cells, or blastomeres, enclosing a segmentation cavity or blastocoel.

This is the structure of the Coelenterate blastula, and the characteristic first stage of the Metazoa. The blastula becomes converted into a gastrula, or the two-layered state, by delamination or invagination. If by delamination—that is to say, by the cells of the blastula budding cells into the interior which are arranged to form the inner layer—the segmentation cavity is converted into the enteron, and an opening is made at the vegetable pole to the exterior, an opening termed the blastopore. If by invagination, the segmentation cavity is more or less obliterated by the invagination of the vegetable pole of the blastula, and the opening which results in the process is the blastopore (see fig. 16). In the Coelenterata both methods are to be found. Among the invertebrate Metazoa the invagination method, or a modification of it, is characteristic, and in this respect they are followed by Amphioxus. Gastrulation,

it is to be noted, is the process which converts the single-layered blastula into the two-layered condition, into the ectoderm and the endoderm of the Metazoon, and the cavity it contains, bounded by the endoderm, is the rudiment of the alimentary canal, the enteric cavity.

In the case of Amphioxus, even at the final stage of the blastula the ectodermal cells are small and are called ectomeres, and the endomeres are fewer and larger at the vegetable pole.

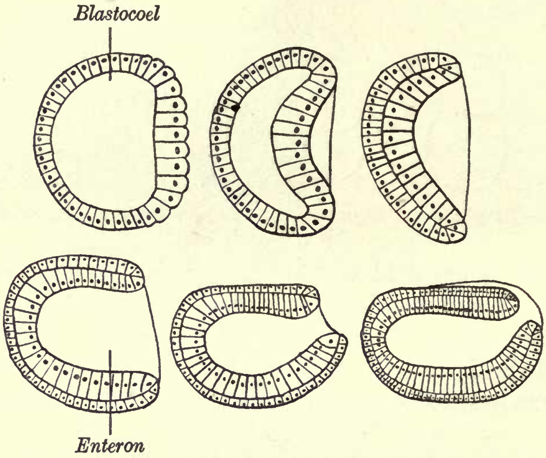


Fig. 69.—Amphioxus. Gastrulation. After Hatschek.

The cells around this patch continue to grow more rapidly than the others, and as a result the vegetable pole becomes flattened and is carried into the interior. The process continues until the endoderm cells apply themselves to the inner face of the ectoderm and the segmentation cavity disappears. The new cavity is the enteron, and its opening the blastopore. This is the gastrula, and it consists only of the two layers mentioned. The blastopore at first is a wide opening, and the enteron a shallow cavity, but the growth at the margin continues to be manifested and in increasing degree. As a result of the multiplication of cells, the blastopore gradually narrows and the gastrula elongates. It thus loses its radial symmetry, and a bilateral symmetry becomes apparent. The growth of

the blastoporal rim is more strongly manifested dorsally at the region which is called the dorsal lip, and a flattening of the embryo takes place just in front of this part of the blastopore. This is the prelude to the formation of important organic systems. It is plain, moreover, that at this stage the animal pole is anterior, the blastopore posterior, and dorsal and ventral surfaces and right and left sides are defined. The conversion of the radial gastrula into the bilaterally symmetrical state may be distinguished by using the term postgastrula.

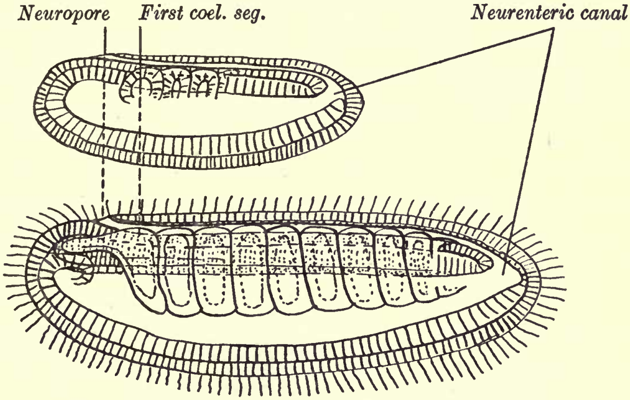


FIG. 70.—Amphioxus. Lateral views of embryos with three and nine coelomic segments. After Hatschek.

The flattened dorsal ciliated area is the primitive neural plate, and the correspondingly flattened endoderm below is destined to be the anterior end of the notochord. Growth continues by the multiplication of cells at the blastopore rim, and the postgastrula gradually increases in length, and the areas mentioned are extended along with the rest of the ectoderm and the endoderm; and as the embryo increases in length the organs are formed from the layers in front. In other words, cells are being constantly formed posteriorly and are differentiated in regular order in front.

The ectoderm is resolved into a dorsal neural plate continuous in front and laterally with the general ectoderm, and all this ectoderm is being gradually extended by the growth

activities of the lips of the blastopore. The cells which enter into the formation of the dorsal plate gradually enlarge, while the ectodermal cells immediately outside them decrease in size. The neural plate cells not only enlarge, but the plate is bent downwards, together with the endoderm below, with the result that a shallow groove is produced, the medullary or neural groove. As this is happening, the neural cells become sharply marked off from the lateral ectoderm cells in the neighbourhood of the blastopore. The latter then commence to grow over the neural plate and ultimately meet and fuse, thus shutting off the neural plate from the exterior. The process begins in the neighbourhood of the blastopore and extends forwards, but, anteriorly, an opening is left which allows the neural groove to communicate with the exterior. This opening is the neuropore, and there the neural layer and the ectoderm of the body maintain their original continuity. The procedure begins on each side of the narrow blastopore, and as a result of the rising and fusion of the ectoderm the blastopore is shut out from the exterior. The blastopore is thereby converted into the neurenteric canal.

Underneath the covering of ectoderm the neural plate is rotated upwards laterally, and the two ridges meet and fuse dorsally, thus converting the neural groove into the ciliated neural canal. The neural canal is therefore a tube open in front at the neuropore and communicating posteriorly by the neurenteric canal with the enteron. The neurenteric canal lies behind the differentiating notochord and persists to a late period of growth. The neural plate by this process is gradually converted into the nerve cord.

The mesoderm is derived entirely from the dorsal part of the endoderm. The median flattened part of the roof becomes grooved, and the lips meet and fuse to form the notochord. As it is gradually separated in antero-posterior direction the cavity of the groove disappears, and the notochordal cells, at first few in number, form a solid longitudinal cord situated between the enteron and the nerve cord. The differentiation begins when about eight somites are formed in the region which marks the beginning of the postgastrular growth.

The advent of the notochord is accompanied by that of

the coelomic segments. The coelomic segments arise as paired expansions of the endoderm on each side of the notochord. The first pair originate with the primitive front end of the notochord. The successive pairs of pouches remain for a short time in communication with the enteron, but successively they are separated by a fusion which restores the enteron after these structures have been developed.

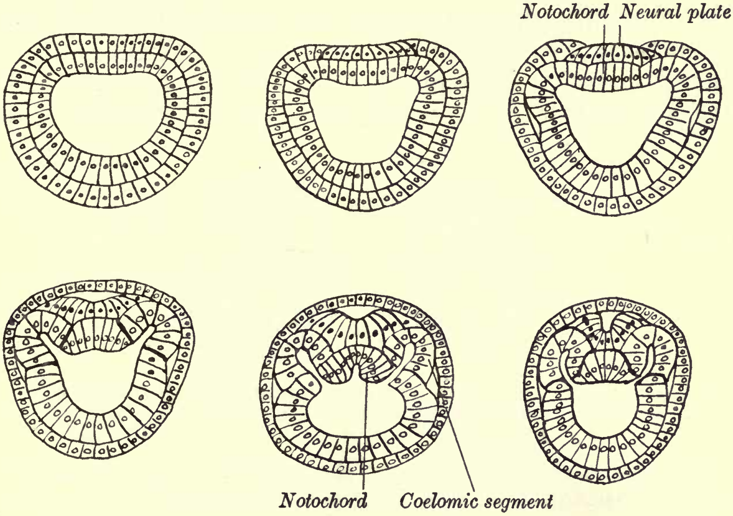


FIG. 71.—Amphioxus. Transverse sections to illustrate the formation of the nerve cord, notochord, and coelomic segments. After Hatschek.

The walls of the somites are applied, the internal to the nerve cord, notochord and endoderm, and the outer to the ectoderm. The pouches extend downwards until they meet below the endoderm, where they mutually form a mesentery. This mesentery is absorbed, and a constriction separates the pouches into a dorsal and a ventral cavity. The upper in each is the myocoel and retains its meristic segmentation; they form the series of somites or myotomes. The lower is the splanchnocoel, and becomes a continuous cavity by the absorption of the walls which separate them. The coelom is thus separated into the dorsal segmental myocoels and the ventral splanchnocoel, which is the body cavity as usually

understood. The body cavity extends from near the front of the enteron backwards, and the peritoneum of which it consists is resolved into a visceral layer around the endoderm, the splanchnopleure, and a parietal layer next the ectoderm, the somatopleure.

The inner wall of the myotome is expanded to form the muscle fibres, and the outer wall is applied to the ectoderm to form the connective tissue of the skin, or dermis. During this formation the myocoel extends downwards outside the splanchnocoel so as completely to furnish the body with the lateral series of myotomes and the dermis. At the side of the notochord each gives out an outgrowth, the sclerotome,

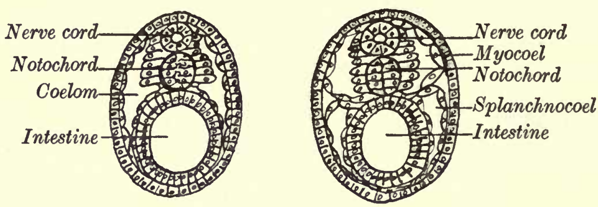


FIG. 72.—Amphioxus. Transverse sections illustrating the division of the coelomic segment into myocoel and splanchnocoel. After Hatschek.

which grows upwards between the notochord and the muscle layer of the myocoel and furnishes the sheaths of the notochord and the nerve cord and the myotome connective tissue (fig. 64). The myocoel not only provides the muscles but the connective-tissue septa for their origin and insertion. Dorsally a similar outgrowth of the myocoel supplies the connective-tissue supports of the dorsal fin. Later the lower edges of the myocoel give rise to the supports of the ventral fin.

The part played by the myocoel does not end with this. Germ cells appear in the wall of the myocoel just ventral to the sclerotome. They are formed close to the anterior septum, and as they grow they project into the cavity in front in each case. They are finally separated as special diverticula containing the gonads.

Before all this has happened with reference to the myocoel the dorsal part of the embryo is rotated forwards, and in association with the rotation a proboscis is formed. The anterior

projection is accompanied by a prolongation of the notochord beyond its original anterior limits, and by hollow outgrowths of the first pair of myocoels. At this period also the anterior end of the enteron is constricted off and divides below the proboscis into two cavities. These are the right and left head cavities. These coelomic spaces, developed independently of the rest of the coelom, are with good reason believed to represent in Amphioxus the head cavity or cavities of the Hydrocoela. Their fate in Amphioxus is of interest. The right cavity increases, and its epithelium becomes flattened to form a coelomic space in front of the enteron and below the notochord. It remains as a closed cavity. The left cavity retains

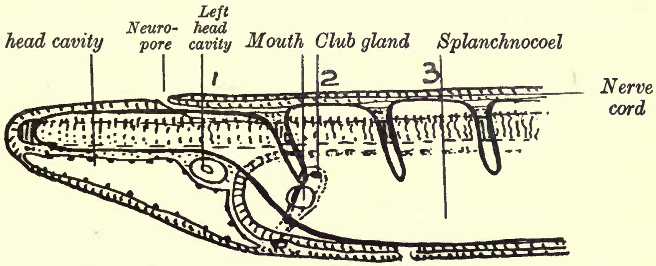


FIG. 73.—Amphioxus. Head of larva, to show the relationship of the first three myocoels to the splanchnocoel and position of the head cavities.

its cylindrical ciliated epithelium and remains a small cavity. At the beginning of the asymmetrical larval period it establishes an opening to the exterior on the left side in front of the mouth, and is thus converted into the preoral pit. It is gradually carried to the median position below the notochord, and the ectodermal part of it increased by a groove. It becomes associated with ciliated folds of the oral cavity which form the wheel organ.

It will be plain from the foregoing account and the figures that the development during the early symmetrical phase is very different from that of the Invertebrates. Up to the time of the formation of the gastrula there is nothing to remark except the absence of mesenchyme. Thereafter the developmental changes are different in every respect. The dorsal

nerve plate maintains its dorsal position and is carried backwards mid-dorsally, and after the formation of the neurenteric canal it is lengthened as a tube. All the mesoderm is derived from the dorsal aspect of the endoderm and is resolved into the entirely new formation, the notochord, and coelomic segments. In the case of the paired somites the early segmentation is noteworthy, and the differentiation into myotomes and body cavity. It is also to be observed that the germ cells appear in the myocoel.

The larva bursts out of the egg membranes just after the differentiation of the mesoderm commences. It is ciliated

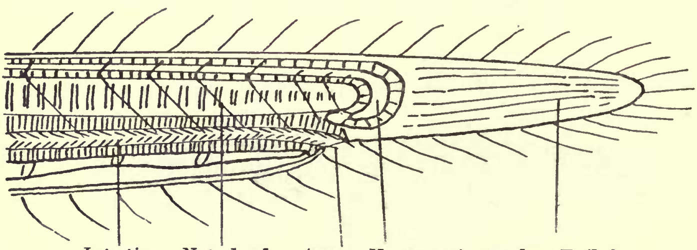


FIG. 74.—Amphioxus. Hinder end, illustrating the position of the anus shortly after its formation and the shutting off of the neurenteric canal. After Hatschek.

all over, and the cilia maintain it in the pelagic state. In the Mediterranean it takes only about eight hours to reach this stage, and the larva is not yet able to feed. During the next twenty-four hours it gains in length and, forming a mouth, anus, and a gill slit, enters upon the larval period proper, but as a larva which is characterised by a remarkable asymmetry affecting the anterior ventral region of the body.

The mouth is formed on the left side by the breaking down of the two layers, and the opening gradually widens into a large oval aperture. At the posterior end of the larva the neurenteric canal becomes cut off from the enteron, and the end of the intestine, thus freed, bends downwards to meet and fuse with a slight diverticulum of the ectoderm and an anus is formed. The larva is provided with a gill slit which appears, like the mouth in front of it, by an absorption of the two layers as a rounded opening situated on the left of the

ventral surface. During the growth of the larva the distortion increases and the gill is carried to the right side. The first gill is followed by the appearance of a succession of gills, and the fifteen gills thus formed all belong to the left side, but are actually on the right side of the body. Later, but during the formation of the series of the gills of the left side, the gills of the right side begin to appear. They are formed high up on the right side above the left gills, and the primitive median line lies between the two sets of gills. As the right gills grow they press the left series of gills around the ventral aspect of the body to the left side. Only eight gills are developed on the right side, and the first of the left series, together with the last six, are suppressed, so that eight pairs occur. These primary gills are widened and divided by tongue bars into two each.

Two further organs are developed in association with the anterior endoderm. One of these is the club-shaped gland which arises as an outgrowth of the endoderm on the right side, opposite the dorsal margin of the mouth. It forms a tube which extends downwards and forwards to an opening which it makes in the ectoderm on the left side in front of the mouth. The tube is therefore open at both ends. It has only a temporary existence, and disappears with the first gill of the left side. The morphology is not at all clear. The second organ originates as a V-shaped thickening of the front endoderm, the angle of the V being directed to the actual median line between the two sets of gills. It is from the beginning glandular and ciliated, and the thickening is extended backwards as the endostyle. From the position of the primitive endostylar modification of the endoderm the actual mid-ventral line is seen to be high up on the right side, and it is possible that the club-shaped gland represents in a fleeting manner the left collar cavity, or hydrocoel, of the Echinoderms. It tends to encircle the mouth as does the hydrocoel of the Echinoderm, and it establishes a communication with the exterior, and the mouth as in the Echinoderms is on the original left side.

After about three months of larval life the asymmetry is gradually corrected. The gills occupy normal positions on

each side of the body, the mouth is rotated forwards, and two oral folds develop which form the oral hood, and the original mouth is narrowed to become the velum. The gills are protected by folds of the ectodermal wall which are produced on each side of a ventral groove and fuse beneath them to enclose the atrial cavity. Just before their formation ectodermal invaginations at the morphological upper part of the gills grow inwards to be developed into the protonephridia.

The animal is now ready to begin its burrowing life, and as it grows the gills are increased in number posteriorly. During the growth the last trace of the neurenteric canal disappears and a short tail is formed into which the endoderm does not penetrate, but all the other elements of the dorsal lip are produced.

It has already been remarked that one of the peculiarities is the absence of mesenchyme. Such is formed during growth from the coelomic mesoderm and gives rise to the connective tissues other than those which are primarily developed from the myocoel. The primary body cavity is represented mainly in Amphioxus by the very primitive blood and blood circulatory system, and it is to this that the solenocytes of the protonephridia are related. The predecessors of Amphioxus, the Hydrocoela, possessed a water cushion as an anterior buffer. The water cushion is certainly developed in Amphioxus in the head cavity, but it is reinforced by the gelatinous skeleton of the notochord which is carried forwards to support the proboscis. Another feature of interest is the concentration of the veins to the meeting-place behind the gills, and the hint of a heart there in the region where the blood is propelled into the gills.

CHAPTER IX

PISCES

Phylum VERTEBRATA
Sub-Phylum CRANIATA *Type*
Class PISCES . . . . Raia

AMPHIOXUS, as we have seen, has no distinct brain, nor is a skull developed. The only skeletal tissue is the notochord and the bars which distend the mouth and support the delicate gills, and it is of a simple gelatinous character. The Craniata have a brain which stands out from the rest of the central nervous system, and a skull. The skull in the lowlier members of the series is made of cartilage, and in the higher it begins in cartilage and is more or less completely replaced by bone. Except the lampreys and hags, the Craniates possess typically two pairs of limbs, and, however modified, these can always be recognised as pectoral and pelvic. In the limbs a cartilaginous skeleton is developed which in the higher Craniates is replaced by a skeleton of bone. Similarly, a jointed skeleton of cartilage, the vertebral column, which may also give place to bone, is developed around the notochord.

The skate, genus Raia, does not correspond to our ideas of the form of a fish. Most fish have a fusiform shape. The head passes into the greatest thickness of the body, and the body tapers again to form the tail. Locomotion is produced by the action of the long muscular tail with the aid of the caudal fin, which is a vertical expansion of its terminal margin. In such a fish it will be seen that the body may be divided into head, trunk or body, and tail. The trunk bears the paired pectoral and pelvic fins, and in addition there are median

fins on the body and tail, and these vary in position and number according to the fish. The median fins are resolved into dorsal, caudal, and ventral. The ventral fin, or fins, is sometimes and unfortunately called the anal fin or fins, because it or the first of the ventral fins lies behind the anus, and the name ventral is given by the same writers to the pelvic fins.

The skate, in association with a leisurely life on the mud and sand at the bottom of the sea, has become flattened. The tail has lost its locomotory power, and the pectoral fins have been greatly expanded with their muscles to act as propelling organs. During its early development in the egg, however, the skate is like other fish and is actually laterally compressed. The change, as will be observed from fig. 75, is initiated by the expansion laterally of the paired fins and especially of the pectoral fins, and this is followed by a flattening of the body and head.

Skates and rays feed principally on Crustacea and fishes. They are found in all seas, and they have been procured also from great depths, 500 to 600 fathoms. They are common in moderate depths, and are landed by fishermen at most ports. The common grey skate of British seas is *Raia batis,* and it attains a great size and weight. The smaller rays, as *Raia clavata,* the thornback, *R. radiata,* the starry ray, are also landed in large numbers, and such are more useful for laboratory work. The attempt should be made with the aid of systematic works on fishes to identify the species, but the identification is not always easy, for rays are liable to a great deal of variation and the distinction between them is sometimes very slight. Fundamentally and essentially they are all the same in structure, and the following description will apply to them all, and even allow of the dissection of their allies, the dogfish, being followed.

Skates are sometimes obtained bearing the large external parasite, the skate leech, *Pontobdella muricata* ; it belongs to the class Hirudinea. In the gills the trematode parasite *Onchocotyle appendiculata* is sometimes observed, and parasitic copepod crustaceans may be found in the nasal sacs.

External Characters.—The body is flattened and rhomboidal in shape. The tail is long and narrow and leaves the

body abruptly. The immensely developed pectoral fins contribute in great degree to the breadth, and the girdle joining the fins may be distinctly seen and felt in the mid-ventral region of

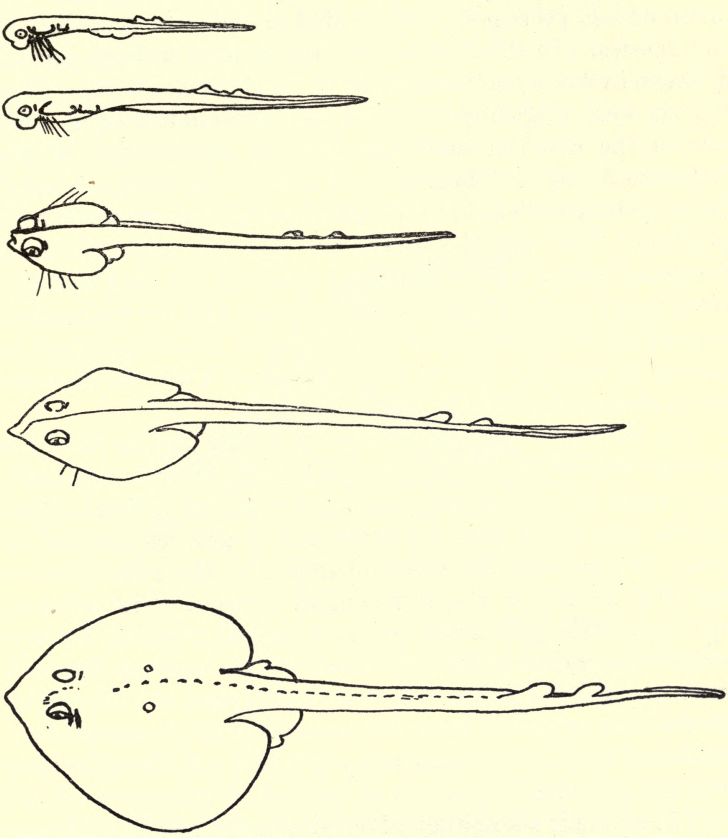


Fig. 75.—*Raia clavata.* A series of embryos to illustrate the change from the early round condition to the flattened state. The figures show also the change in position of the dorsal fins produced by growth, the disappearance of the ventral median fin, the expansion of the paired and especially of the pectoral fins. The external branchial filaments are also indicated. From a series kindly lent by Mr. R. S. Clark.

the body. The pelvic fins are much smaller, and are placed on each side posteriorly between the pectoral fins and the tail. There are two small dorsal fins near the extremity of the tail, but it will be seen from fig. 75 that in the embryo they are

situated far forward on the dorsal surface. A small caudal fin occupies the upper surface of the end of the tail. A ventral fin is absent, but it is present in the embryo. The anterior angle is supported by a rostral extension of the skull, and it is more or less prominent and pointed or rounded, according to the species. In the skates it has the form of a sharp-pointed process, in the rays it is rounded.

The eyes, originally lateral in position as in fishes generally, are in the adult situated dorsally, one on each side of the flattened head; and behind them are the spiracles, a pair of large openings which have likewise been moved from a lateral position. The spiracles open into the pharynx. Each is furnished with a valve, and these openings are used to introduce water to the pharynx, and so to the gills for respiration. According to circumstances, the water so introduced may be passed through the gills to the exterior, or it may be returned to be ejected through the spiracles.

On the under side the transverse mouth lies far from the anterior end of the body. The jaws are furnished with many rows of teeth. The nasal openings are placed in front of the mouth, with which they are connected by grooves bounded by lips. The rectangular space bounded by the nasal grooves and the mouth is the fronto-nasal process. The external openings of the gills are a paired series of five slits, the two series converging posteriorly towards the median line. A rudimentary sixth slit is sometimes quite plain as a depression of the skin which covers the ventral part of the pectoral girdle. Except this rudimentary gill slit, all the gills open into the pharynx.

The cloaca is a longitudinal opening in the mid-line between the pelvic fins, and a pair of abdominal pores may be seen near its hind margin.

Sensory tubes or mucous canals and their apertures are plainly visible on the under surface. The canals, which radiate over the pectoral fin from a region near the anterior pair of gills, are usually prominent, and others may be traced between the mouth and the rostrum.

The male is distinguished externally by bearing distinct processes of the internal borders of the pelvic fins. These are

called claspers, and are used for conveying the sperms of the male into the oviduct of the female. The male possesses frequently a patch of spines on the dorsal aspect of the pectoral fin. A further distinction is that in the male the teeth are sharp and pointed, while in the female they are more flattened.

The skin or integument consists of a many-layered epidermis or ectoderm based on a basement membrane and supported by a connective-tissue layer or dermis, and though thin it is very tough. Imbedded in the dermis are the bases of the sharp-pointed scales. These originate as plugs of dermal cells which indent the epidermis. The dermal cells then enter

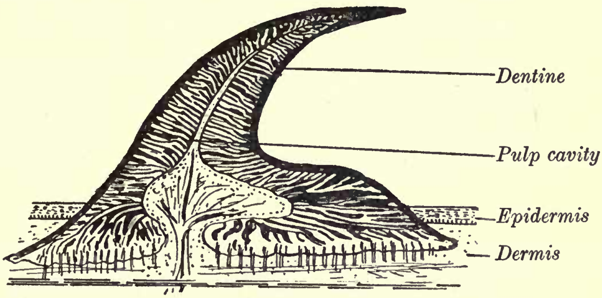


Fig. 76.—Raia. Placoid scale in longitudinal section.

upon a process which is exactly similar to tooth formation. The cells next the ectoderm are called odontoblasts, and lay down next the ectoderm a matrix in which lime is deposited, thus forming a hard and resistent layer of dentine in the form of a cup ending apically in a sharp point. This is succeeded by the formation of further layers internally to the first, and thus the inner or pulp cavity is gradually narrowed. The scale is thickened internally, and extended below at the margin of the cup. As it grows it is pushed through the epidermis and forms the small or the large placoid scales so characteristic of the Elasmobranch fishes. The pulp cavity in the process is reduced to a narrow canal from which branching canals radiate outwards through the dentine. Below, the pulp cavity maintains a wide expansion, and the dentine is laid down even more like bone in the formation of the basal plate. Placoid scales are prominent usually on the dorsal surface,

and reach a large size in some species, as the thornback and starry ray. Their position and the rows which they form are important features in determining species. The scales may also occur on the ventral surface.

Internal Structure.—Bony formation is thus evidenced in the development and structure of the placoid scales. The skeleton, however, is a cartilaginous one, and it remains cartilaginous, only strengthened by superficial calcifications in the skull and in the centra of the vertebrae. Cartilage is a connective tissue in which a matrix is formed between the cells and changed chemically with the formation of the compound

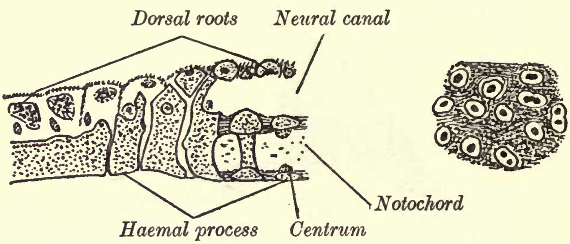


Fig. 77.—Raia. A portion of a sagittal section of an embryo skate, illustrating the relationship of the arches of the vertebral column, and a more magnified part of one of the arches to illustrate its histological structure.

called chondrin. The cells have the power of multiplication, and thus the cartilage may be enlarged as required. It forms a tough, resistent, elastic tissue, and it is not penetrated by blood-vessels nor by nerves (fig. 77). It is developed primarily in the sheaths around the notochord and nerve cord and in the head region.

Skeleton.—The skeleton is resolved into axial and appendicular. The axial consists of the vertebral column, ribs, and skull; the appendicular, of the skeleton of the limbs and their girdles, and of the median fins and their supports.

The vertebral column is developed in the products of the sclerotomes which ensheath the notochord and the nerve cord, the notochord being surrounded by an inner perichordal sheath and an outer skeletogenous sheath. In many fishes the chondrification takes place in a series of neural and haemal processes, confined in the case of the notochord to the skeleto-

genous sheath, and as they expand these processes meet and fuse to form centra or bodies around the notochord and arches around the neural canal. In the skate the perichordal sheath of the notochord is chondrified early, and the rings of cartilage thus formed are the centra. The neural and haemal processes are formed independently, and secondarily fused with the centra and with one another. Even in the case of the species in which arch centra are developed the inner sheath of the notochord is invaded by the cartilage.

The rings around the notochord become thickened by cartilaginous development, and the notochord is correspondingly reduced. The constriction of the notochord takes place, however, only in the middle of each ring, and the cartilage is further

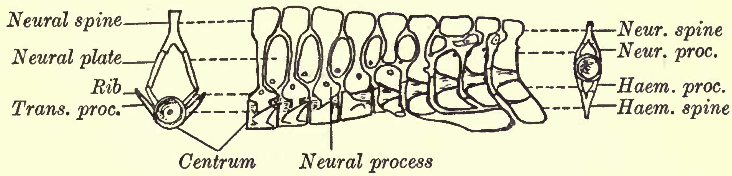


FIG. 78.—Raia. The vertebral column of *R. radiata* at the hinder end of the body and the beginning of the tail, with end views of a body and a tail vertebra.

strengthened by calcification. The centra thus take the shape of ring-shaped bodies, hollow at each end, and such centra are described as amphicoelous. The gelatinous notochord is thus expanded between the centra and contracted to a thread in each centrum.

The neural canal is invested by the neural processes and by other paired and median plates. The neural arch processes are perforated by the ventral roots of the spinal nerves. Laterally a series of plates are formed, neural plates, and these are each perforated by the dorsal root of the spinal nerve. The arch surrounding the canal is completed by roofing spines. The neural spines and the neural processes are in some of the rays, at least, connected by bars which alternate with the neural plates. The haemal processes developed in association with the neural processes form transverse processes in the trunk region which usually bear small ribs. Behind the body cavity the haemal arches project downwards, and an arch, the haemal

arch, is formed by the co-operation of haemal spines. The haemal arch encloses the caudal artery and vein.

That portion of the vertebral column from the region of the pectoral girdle forwards to the skull is converted into a single mass of cartilage perforated merely for the roots of the spinal nerves. In that part of the vertebral column also, as in the skull in front of it, the notochord is reduced to practical if not complete extinction. This change is to be regarded as being associated with the relative immobility of that part of the body.

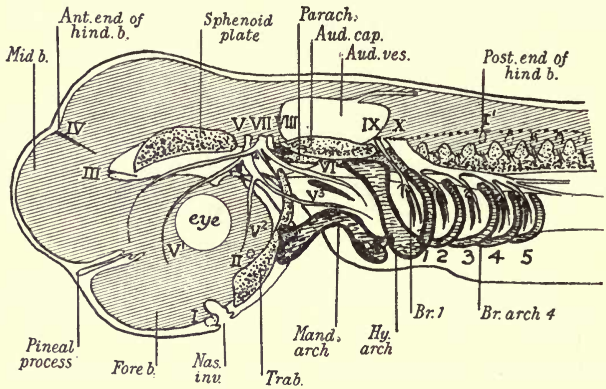


FIG. 79.—Acanthias. The early condition of the chondrocranium. The cartilaginous vertebral column, parachordals, trabeculae, and sphenoid plates are indicated by dots, the visceral arches by heavier shading. The nerves are shown and numbered. Modified after Sewertzoff.

The skull consists of a brain case, or chondrocranium, developed round the brain, and a series of arches developed around the anterior end of the alimentary canal.

The chondrocranium originates in a pair of cartilaginous bars, one on each side of the notochord: these are the parachordals; and in a pair of cartilages which extend forwards from the anterior end of the notochord, the trabeculae. As the front end of the head is bent downwards at this stage, these elements, to start with, are placed at about right angles with one another (fig. 79). The angle between them is marked by the position of the infundibulum of the brain. With the appearance and expansion of the parachordals and trabeculae another pair of

plates are formed laterally, the sphenoid plates. Around the auditory organ, beginning basally, a cartilaginous capsule is formed, and similarly the nose on each side is invested in a dome-shaped capsule. The parachordals expand up the side of the brain and fuse with the auditory capsules. The trabeculae, gradually rotated into the plane of the parachordals, likewise expand and fuse with the nasal capsules and the sphenoid plates. The result is a cartilaginous trough for the brain carried forwards as a rostrum, and to which the nasal capsules and the auditory capsules are fused as wings. The roof is invested only

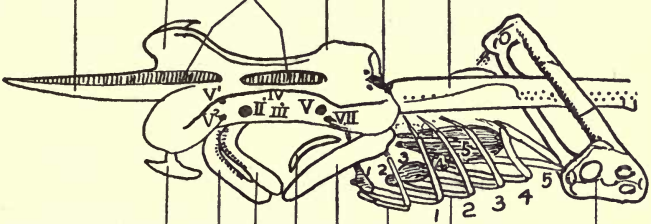


FIG. 80.—Raia. Diagrammatic view of the chondrocranium, visceral arches, and the pectoral girdle of the adult skate.

between the auditory capsules and by a narrow bar between the nasal capsules, and thus it presents anterior and posterior fontanelles. The brain case opens into the neural canal by the foramen magnum. As it develops, the cartilage of the brain case surrounds the nerves emanating from the brain, and nerve foramina are thus formed.

The series of arches, called visceral arches, developed around the anterior end of the alimentary canal are the mandibular, hyoid, and five branchial arches, all paired. The mandibular arch is divided to form the upper jaw or palatoquadrate cartilage and the lower jaw or Meckel's cartilage. The hyoid arch yields the hyomandibular cartilage which suspends the jaw cartilages to the auditory capsule. The lower part of the hyoid is resolved into three segments, epi-, cerato-, and hypo-hyal.

The epihyal is connected to the hyomandibular by a ligament, and the hypohyal to the first hypobranchial. The branchial arches are divided up into four segments each, pharyngo-, epi-, cerato-, and hypo-branchials. It will be observed that the ventral elements of the first and the fifth arches fuse with their neighbours, and that the fourth and fifth arches fuse with one another dorsally on each side. The fifth arch also is attached to the pectoral girdle (fig. 80). The spiracle lies in front of

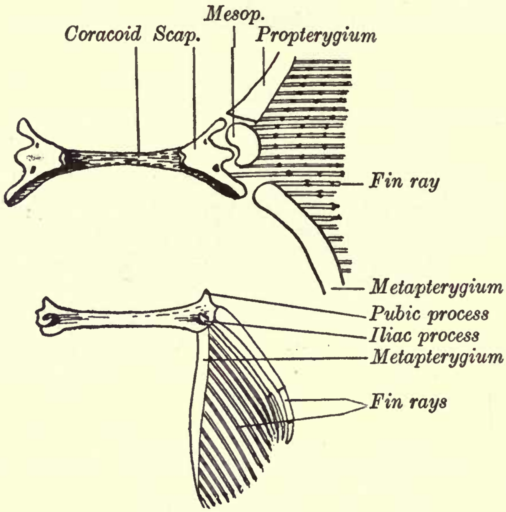


FIG. 81.—Raia. Dorsal view of the pectoral and the pelvic girdles.

the hyoid, the first branchial cleft between the hyoid and the first branchial arch, and so on.

In addition to the cartilages mentioned, there are others which are developed in regions requiring extra support or in positions which suggest they may be of interest as rudimentary evidences of pre-existing arches or structures. Such are the labial cartilages developed in relationship to the upper and lower jaws, the spiracular cartilage developed in front of the hyomandibular. The extrabranchial cartilages appear to be rather Elasmobranch than historical in their nature.

The paired fins are heralded by the appearance of horizontal and practically continuous ridges of the sides of the body of

the embryo, the ectoderm being thickened and the somatic mesoderm multiplied. These are accompanied by the formation of buds of the myotomes, which yield an abundant mesoderm and ultimately the muscles of the limb in each case (fig. 93).

The pectoral fins are connected by a girdle of cartilage. The pectoral girdle consists of a dorsal scapula and suprascapula on each side, the suprascapulae almost meeting to be attached to the expanded crest of the fused region of the vertebral column. The scapula on each side, after giving articulation to the elements of the fin, passes below into a bar which extends across the ventral body wall to meet and become continuous with the scapula of that side. This is the coracoid. Three facets are provided on each side for the articulation of the pro-, meso-, and meta-pterygia, and to these the long fine fin rays are articulated.

The pelvic girdle consists of a bar of cartilage which lies transversely in the ventral body wall at the hinder end of the body. This is the ischial bar, and at each end it is produced into an anterior pubic and an upwardly directed iliac process. At each end also two facets are provided for the rays and the metapterygium. In the male, as has already been observed, the inner part of the fin is highly modified and enlarged to form the clasper on each side.

The median fins are supported by basal plates which connect them to the caudal vertebrae.

Alimentary Canal.—The alimentary canal in all vertebrates is almost entirely derived from endoderm. It is only the anterior part of the mouth which has a stomodeal origin, and only a part of the cloaca which has a proctodeal origin.

In the skate the cartilaginous jaws bear numerous teeth in parallel transverse rows. They are renewed on the inner side, gradually rotated to the opposing surface and lost on the outer surface. The teeth are developed as the placoid scales. But in this case the formation is associated with the appearance of a prolongation of the inner ectoderm of the mouth into the dermis as a dental band. The dental band internally is formed into cups, each of which encloses a cone of dermis. The dermal cells next the ectodermal cup, or odontoblasts, proceed

to form dentine. During their development the teeth are gradually rotated along the inner side of the dental band, the dentine gaining in thickness and the whole tooth in size.

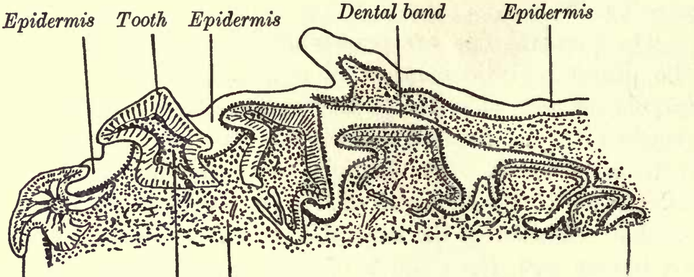


FIG. 82.—Development of teeth of Myliobatis. After Rose.

Finally it reaches the jaw epithelium, which it pierces. In structure it is exactly the same as the scale, presenting a strong surface of hard dentine graduating internally into a more alveolar condition invaded by canals from the pulp cavity. The canals have the structure and relationship of Haversian canals of bone. It has been said that the ectoderm is able to form on the tooth and on the scale an enamel crown, but it is more probable, as Rose said, that the teeth of the Elasmobranchs are, like the teeth of the Edentate mammals, devoid of enamel.

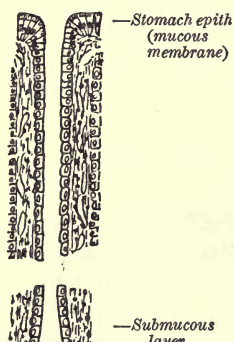


FIG. 83. — Raia. Gastric gland in longitudinal section.

The mouth cavity expands into a spacious pharynx in which may be observed the inner openings of the spiracle and the branchial clefts. Behind the last branchial opening the pharynx narrows to form the oesophagus or gullet. The canal expands slightly to become the stomach, which is bent gradually into a curve, and is thus resolved into a proximal cardiac and a distal pyloric region. The mucous epithelium of the stomach

is produced into the submucous layer to form numerous, simple, tubular gastric glands (fig. 83). The walls of the stomach are strongly muscular. The opening between the stomach and intestine is tightly closed by a constricting ring of muscle, a sphincter muscle. Beyond the pylorus the intestine is narrow for a short distance, and this part of the intestine receives the bile duct from the large trilobed liver and

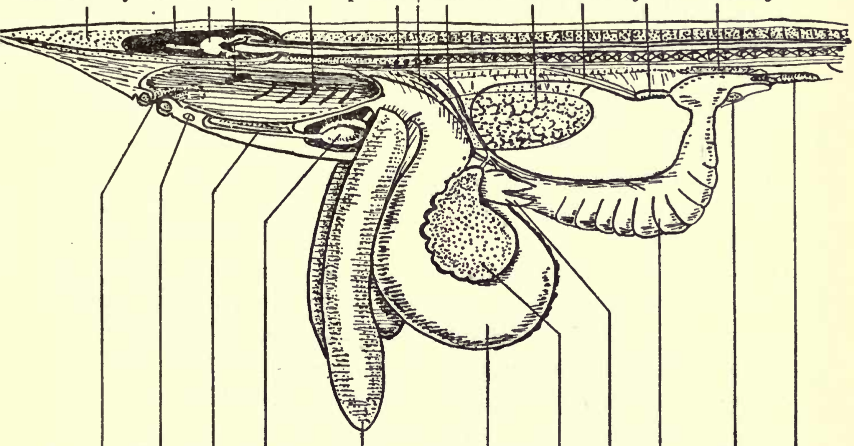


FIG. 84.—Raia. General dissection from left side.

the pancreatic duct from the pancreas. A gall bladder is situated between the right and middle lobes of the liver and serves as a reservoir for the bile. The pancreas is light yellow in colour and is placed around the pylorus. Beyond this region the intestine expands into a wide tube which leads to the short rectum. Internally the wall is folded in the form of a spiral valve which serves to increase the absorptive area and to give time for digestion and absorption. The terminal end of the intestine, the rectum, is produced into a distinct cylindrical body supported by mesentery, the rectal gland.

The food is rapidly conveyed from the mouth to the stomach. In the stomach it is subjected to an acid digestion by the action of the gastric juice, and in the intestine to an alkaline digestion by the products of the liver and pancreas. The digested products are absorbed by the vessels of the intestine, and the undigested residue is egested at the cloaca. The liver, the pancreas, and the other glands of the alimentary canal are developed as outgrowths of the primitive endoderm.

The **respiratory organs** are the gills. The spiracle possesses a rudimentary gill on its front wall, and it is supported by the spiracular cartilage. The first four branchial clefts bear gill filaments on both the anterior and the posterior walls, the fifth cleft only on the front wall. The cartilaginous gill arches intervene between the clefts, and support the gill folds internally. So that from the point of view of the arches the hyoid arch bears one set of gill filaments, or a hemibranch, the next four a pair of gills each, and the fifth arch does not support a gill. The gills are contained in a spacious gill chamber which is interrupted by folds dividing the chamber into a series of clefts and which bear the filaments on the opposing faces. The gill filaments are further supported by gill rays which spring from the arches. These are internal gills, and are endodermal in origin. In the embryo the external margins of the gills are produced as fine long outgrowths forming external gills which protrude from the apertures of the gills into the cavity of the egg.

In fishes, generally, the water is introduced to the gills by the mouth, and expelled after passing over the gills. In the skate the water is carried in through the spiracle, and it may be passed out from the gills or returned to the spiracle for discharge. The blood is carried in the venous condition to the gills, and it comes into close relationship with the water by being spread over the thin epithelial surface of the gill filaments. The oxygen borne by the water is taken up in exchange for carbon dioxide, and other products of metabolism which can be readily dealt with at such a surface, and this is respiration. The haemoglobin of the blood bears the oxygen to all parts of the body.

Coelom.—The skeletal muscular system is derived from the upper division or myocoel of the coelomic mesoderm. This part of the coelom, as in Amphioxus, is resolved into a series of myotomes, the cavities of which open into the general body cavity, or splanchnocoel, below them. As they are cut off in succession from the splanchnocoel the myotomes spread around the body wall outside the splanchnocoel, and their inner layer yields the muscle fibres, while the outer layer is converted into dermic mesoderm. The muscles related to the skeleton of the body and limbs are thus originated but undergo much modification in the body. It is only in the tail that the myotomes retain the primitive meristic segmentation. In the tail, moreover, some of the fibres are shortened and broadened to form together an electric organ which has the appearance of a gelatinous mass embedded in the tail muscles. In the rays it is feebly developed, but in the skate it is more prominent. The torpedo ray possesses a large and powerful pair of electric organs on each side of the head from a similar modification of muscle fibres derived from the muscles of the visceral arches. In other fishes, still other muscles have been modified to produce electric organs as a means of protection. Muscle fibres normally during contraction give rise to an electric current, and these fish have evidently found it possible to so modify the muscle as to produce an intensified current without contraction.

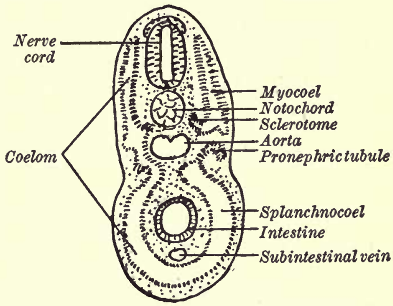


FIG. 85.—Raia. Diagrammatic transverse section of embryo illustrating fate of coelom.

The body cavity, derived as has been said from the splanchnocoel division of the coelom, is in Craniata not segmented. At first it forms a continuous cavity, but it becomes divided into a pericardial cavity and a peritoneal cavity which communicate by a small canal. In the peritoneal cavity, the mesentery is at first continuous, but it becomes absorbed except in the gastric and the rectal region. The gonads are

supported on special mesenteric folds of the peritoneum. These have been called, in the male, the mesorchium; in the female, the mesoarium.

Mesenchyme is yielded from the splanchnocoel mesoderm generally, and the musculature of the visceral arches, as of the viscera, is likewise derived from the body-cavity mesoderm. The mesenchyme is otherwise resolved into connective tissues and into the blood and the vascular system.

The **vascular system** is derived, as has just been said, from mesenchyme. Certain cells are freed as corpuscles, while others are converted into the blood-vessels. The heart and the main vessels are furnished with coats of connective tissue and of muscle. The system is arranged in a heart and a widespread series of arteries leading blood from the heart, capillaries which bring the blood into intimate relationship with the cells of tissues and organs, and veins which return the blood to the heart. Some of the veins are widely expanded, and such are called sinuses. The blood is red-coloured, haemoglobin being contained in the oval, flat, nucleated, red corpuscles, or erythrocytes. The other blood cells are leucocytes and thrombocytes. The fluid in which they occur, the plasma, together with leucocytes, exudes through the capillary walls into the spaces outside them, bearing oxygen and food which thus come into close contact with the cells. The escaped fluid cannot return against the current, and, now called lymph, it is collected in spaces of the mesenchyme. These spaces communicate with better-defined spaces, and the latter with special vessels called lymphatics. The lymphatics restore the lymph to the blood by an opening on each side into the dorsal wall of the precaval sinus, an opening guarded by two valves. The valves open when the pressure of the lymph is sufficient to overcome the pressure of the blood which keeps the valves closed.

The circulation primarily is concerned in bringing the food material from the yolk into the embryo. The first veins are a pair of vitelline veins which lead from the blastoderm to the embryo and merge to form the heart. In front two vessels are formed which diverge from the heart to encircle the head fold of the gut and turn backwards to supply the embryo. The

aortae shortly fuse to form the single aorta, and the vitelline artery is formed later to lead the blood back to the blastoderm from a point above the pronephros on the right side. The blastoderm thus marks the vascular area of the yolk, and as it extends so do the vessels. The artery extends forwards in front of the embryo and is spread into small arteries and into capillaries. The blood is reassembled into veins which finally open into a vein which occupies the margin of the vascular area. The margin, however, is gradually fused behind the embryo, and consequently the two marginal vessels fuse to

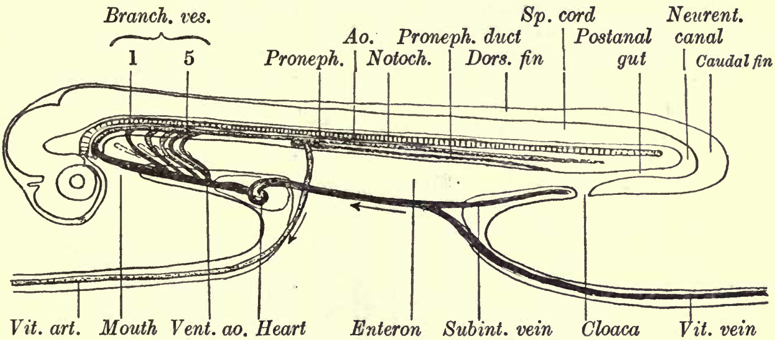


FIG. 86.—Raia. Diagram of the embryonic circulation.

form a single vitelline vein which lies along the primitive streak and leads the blood into the heart. As it passes into the body it comes into relationship with two veins which bring the blood back from the posterior end of the embryo, the subintestinal veins, and these, like the aortae above, fuse to form a single vessel. The other veins described below are gradually formed as the embryo increases in size.

The heart lies in the pericardial cavity—that is to say, just in front of the pectoral girdle. The venous blood is carried into it by the sinus venosus, which runs across the hinder wall of the cavity between the two precaval sinuses. The sinus venosus opens into the auricle by a two-valved aperture. The large, thin-walled auricle transmits the blood to the ventricle, and the opening is guarded by two valves. The thick-walled

ventricle has a smaller cavity, and opens in turn into the conus arteriosus. The conus is furnished internally with three rows of five pocket valves, or semilunar valves, and it conducts the blood into the ventral aorta.

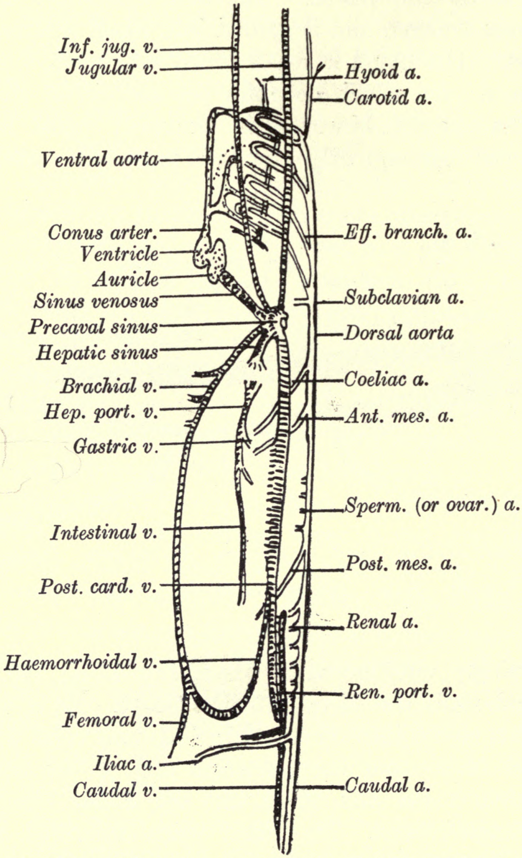


FIG. 87.—Raia. Diagram of the adult circulation, lateral view.

The ventral aorta runs forward in the floor of the mouth below the basal elements of the branchial arches. It gives off near its origin a pair of posterior innominate arteries, each of which divides into three afferent branchials; and distally it divides into a pair of anterior innominate arteries, each of which splits into two afferent branchials. These afferent

branchials run up between the gill slits, sending branches into the gill filaments. The blood is by this means brought into close contact with the stream of water which is being constantly during life passed through the gills, and it is arterialised. The arterial blood is conveyed from the filaments into vessels which loop-like encircle the clefts. There are four complete encircling vessels around the first four clefts, and they are

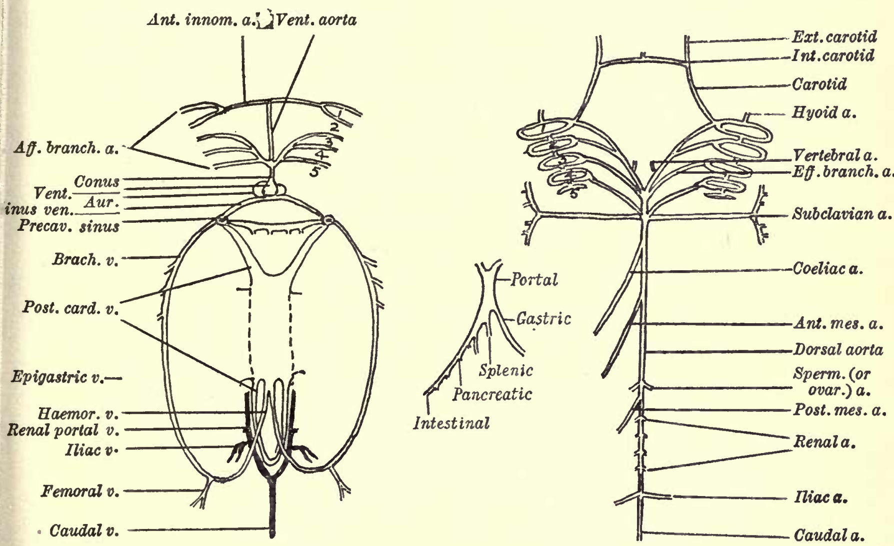


FIG. 88.—Raia. Diagrams of arterial, venous, and portal vessels of adult.

connected by horizontal anastomosing vessels. The fifth arch possesses a half-loop and is similarly connected to the fourth loop. The first loop receives blood from the hyoid. The upper ends of the loops give origin to the efferent branchials, which are directed backwards in the roof of the pharynx to fuse in succession in forming the anterior end of the dorsal aorta.

From the point of origin of the first efferent branchial there arises the common carotid. The common carotid divides into an external and an internal branch. The two internal carotids join below the brain case, and the vessel thus formed enters the brain case through a minute foramen to

supply the brain. A vertebral artery, also from the first branchial, reaches the brain by way of the vertebral column.

The dorsal aorta gives off a pair of subclavian arteries just before it receives the last pair of efferent branchials, and then in succession a series of median arteries which run in the mesentery of the peritoneal cavity. These are the coeliac, supplying the stomach and liver; anterior mesenteric, directed to the pancreas, spleen, and intestine; and the posterior mesenteric, which gives blood to the rectal gland. Paired vessels are supplied to the reproductive organs, kidneys (renal), and to the pelvic fins (iliac), and then the aorta passes on into the tail as the caudal artery. The blood is conveyed by all these branches into capillaries, and these reassemble to form veins.

The blood from the tail is returned by the caudal vein. The caudal vein bifurcates on entering the body to form two renal portal veins. These veins, after receiving branches from the pelvic fin and body wall, send branches into the kidneys. The kidneys thus receive both arterial and venous blood, and this blood is carried away by the renal veins. The renal veins open into the posterior end of the posterior cardinal veins, which lie along the inner border of the kidney and are connected at their posterior ends by an anastomosing branch. In front of the kidney the posterior cardinals fuse to form an expansive cardinal sinus. This sinus receives the blood from the reproductive organs on each side by large openings which transmit the blood from the reproductive sinus—spermatic or ovarian, according to sex. The two cardinal veins emerge again in front, and are directed forwards and outwards to open into the precaval or Cuvierian sinus.

The precaval sinus opens into the sinus venosus of the heart, and it receives besides other important vessels:

(1) The lateral vein brings blood from the pelvic fin. Posteriorly it is directed forwards in the mesentery to enter the cardinal sinus in company with its neighbour, and this portion of the vessel is called the haemorrhoidal. The rest of the vessel is regarded as a fusion of the epigastric and the brachial, which latter enters the precaval sinus at its anterior end.

(2) The blood from the liver is received into a hepatic sinus which opens into the precaval sinus on each side.

(3) The blood from the head is brought into the precaval sinus by two jugular veins on each side.

The blood which is sent to the stomach, spleen, pancreas, and intestine by the coeliac and mesenteric arteries is returned by gastric, splenic, pancreatic, and intestinal veins. These fuse to form a common trunk, the hepatic portal vein. The liver, like the kidney, receives therefore a supply of arterial and venous blood, and the blood is conveyed by the hepatic veins into the hepatic sinus, and so to the precaval sinus. The venous system is somewhat complicated by fusions and expansions of the vessels, but it indicates a type of venous system which in the main is the primitive one of the Craniates.

Endocrine Organs.—A large spleen is placed between the two loops of the stomach, and isolated parts of the splenic tissue may be seen sometimes around the outer border of the stomach. It is derived from mesenchyme of the splanchnic layer of the body cavity, and forms a large organ in which the blood flows in ill-defined spaces. The blood is derived from the anterior mesenteric artery, and is discharged into the portal vein. In front of the ventral aorta a thyroid gland is to be found as a rounded red body. It originates as a diverticulum of the floor of the pharynx in front of the hyoid. It is the homologue of the endostyle of Amphioxus. The duct is lost, and it takes up the position indicated. The thymus is paired and lies on each side just above the gills, and a rudimentary thymus is said to be related to the spiracle. The thymus is developed by bud-like outgrowths of the dorsal angle of the gill clefts. A pituitary body, or hypophysis, is attached to the infundibulum, and both maintain their independence. The infundibulum is an outgrowth of the floor of the thalamencephalon, and the hypophysis is a diverticulum of the ectoderm of the inner end of the stomodeal invagination. The adrenal bodies are small yellow bodies which lie dorsally between the kidneys and in relation to the sympathetic ganglia. Each consists of two parts, one derived from the sympathetic ganglia, and the other from the peritoneum. The former is the medullary chromophile substance, and the latter the cortical substance, of the adrenals of higher animals. In the skate they are independent, the medullary bodies remaining in connexion with the

sympathetic ganglia, and the cortical forming a long structure on each side, just internal to the kidney.

The **central nervous system** arises from the medullary canal of the embryo. The brain is defined by three vesicles, the fore-, mid-, and hind-brain, which originate as expansions of the anterior end of the neural canal. The forebrain is deflected below the midbrain, the roof of which comes thus to occupy the anterior end of the embryo. During this process, which is called the mesencephalic flexure, the forebrain gives off paired diverticula to form the cerebral hemispheres and the optic cups. The cerebral hemispheres, or prosencephalon, are at first hollow, and the cavities they contain are the lateral ventricles; but the walls thicken by the development of neurons which form areas of grey matter and of nerve fibres which form tracts of white matter. The hemispheres arise primitively in association with the nasal cavities, and anteriorly they give off the olfactory lobes which extend forwards and outwards to end over the nasal sac on each side. As the result of the thickening, the cavities or ventricles are obliterated, and only an indication of their communication with the original cavity of the forebrain by the foramina of Monro can be made out.

The forebrain, after giving off the optic cups and the hemispheres, is termed the thalamencephalon, and its cavity the third ventricle. The side walls are thickened, forming the optic thalami. The front wall is the lamina terminalis, the original anterior end of the neural canal. The roof is thin and is produced into the median pineal body or epiphysis, and this remains in the adult as a fine process of the roof. The floor is also thin and is folded into the lobi inferiores and produced into the infundibulum, to which is attached the pituitary body or hypophysis. Between these structures of the floor the three-lobed sacculosus vasculosus may be seen. Transverse fibres connect the thalami antero-ventrally by the anterior commissure, and behind the pineal outgrowth of the roof by the posterior commissure.

The midbrain, or mesencephalon, is expanded dorsally and folded longitudinally to form the paired optic lobes. Below, it is thickened like the remaining part of the brain, and the thick diverging columns of the floor of the midbrain are called

the crura cerebri, or cerebral peduncles. They are important conducting tracts of motor and sensory fibres to and from the forebrain. The central canal of the midbrain is called the iter, or aqueduct of Sylvius.

The iter expands into the fourth ventricle, which is the cavity of the hindbrain. The hindbrain, or rhombencephalon, presents a thin roof except in front, where it is thickened and expanded to form the tongue-shaped cerebellum or metencephalon. On each side in front the walls are folded, forming the restiform bodies, and the floor is thickened in continuation with the spinal cord and the crura in front. The thickening constitutes the medulla oblongata and it contains important centres and tracts. The superior tracts are continuous with the sensory tracts of the spinal cord and the inferior ones with the motor tracts of the spinal cord, and these are directed to the cerebellum and to the forward parts of the brain. The centres of the medulla control the heart and the gills. The cerebellum of the fish is large in relation to the great powers of movement. The cerebellum is closely associated with centres of nerves coming from the auditory organ concerned with movements relating to equilibrium, and with centres of cutaneous nerves. Movements may be produced through the connexions of the cerebellum with cutaneous nerves and the acustico-lateralis system from stimuli reaching it through the lateral line system, the ear, the eye, the nose, or the mouth.

The medulla passes insensibly into the spinal cord, and its ventricle narrows to form the central canal of the cord. The walls are divided by dorsal and ventral fissures into lateral halves containing paired centres and tracts.

The central nervous system shows not merely a differentiation into the various parts of the brain, but primitively a segmentation which has been found to be constant. These segments, which alternate with the primitive segments of the upper part of the coelom or myotomes, have been called neuromeres.

The nerves arise from neurons which send out branches from the medullary canal, and such are motor nerves. Nerves also arise from the neural crest, which is produced as the neural

plate is being folded to form the neural canal. These give rise to ganglia, and the cells send their axons into the nerve tube and also distally. Such are sensory nerves.

The nerves are divided into sensory and motor. The sensory fibres carry stimuli from the skin and sense organs, from the muscles and from the viscera. The motor fibres carry stimuli outwards which produce some effect. They end in the muscles or in glands. The afferent and the efferent stimuli may be related in performing a simple reflex action directly, as, say, through the spinal cord. And all degrees of complexity between a simple reflex and the complex reflexes associated with correlating paths and inhibitory paths have to be considered. Not only so, but the nervous system is liable to stimuli from the endocrine organs through the blood stream.

The nerves are divided into cranial nerves and nerves of the spinal cord, and these are associated also with the sympathetic nerves.

The cranial nerves are :

I. Olfactory.—The olfactory lobes are connected with the sensory cells of the much-folded epithelium of the nose by numerous fibres, the olfactory nerves. On their inner side an accessory olfactory nerve, the nervus terminalis, may be exposed with care and disclosed by sections. It is connected to the brain in the wall of the lamina terminalis and is distributed to the inner aspect of the nasal epithelium. It is provided with a ganglion and appears to be associated with the neuropore primarily[1] (fig. 89, 1′).

II. Optic.—The retina of the eye gives off many fibres which leave the eye by the optic nerve. The nerves meet and fuse below the thalamencephalon, forming the optic chiasma in which the fibres cross from one side to the other. Beyond the chiasma the nerves are absorbed in the thalami. Both these nerves, it is almost unnecessary to say, are purely sensory.

III. Oculomotor.—These are motor nerves which arise in the floor of the mesencephalon and pass into the orbit to supply the superior, inferior, and internal recti and the inferior oblique muscles of the eye.

[1] 1905, Locy, *Anatomischer Anzeiger*, Bd. 26.

IV. Trochlear or Pathetic.—This nerve is motor and arises in the roof of the brain between the optic lobes and the cerebellum. The pair of nerves form a chiasma and pass out from the brain case by a number of small branches which are spread into the superior oblique muscle of the eye.

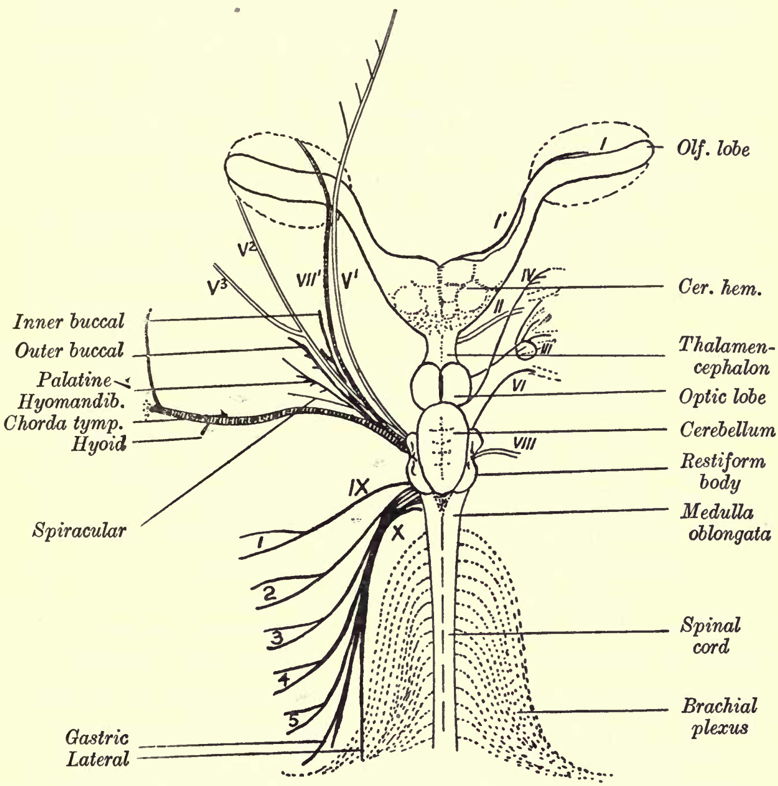


FIG. 89.—Raia. Dorsal view of brain and cranial nerves.

V. Trigeminal.—This nerve originates in a large ganglion, the Gasserian ganglion. Its nerves enter the medulla at its anterior end. Distally the ganglion gives off two branches, the lower of which bifurcates into two. The ophthalmic branch (V^1) passes over the eye muscles in the orbit, becomes united with the ophthalmic branch of the VIIth and is supplied

to the skin of the dorsal region of the snout. The maxillary (V^2) is also associated with the VIIth and runs along the floor of the orbit to reach the integument in front of the mouth. Both these branches are sensory. The mandibular (V^3) accompanies the maxillary for some distance across the orbit and leaves it to enter the mandibular muscles. This branch is motor and is concerned in the innervation of the visceral muscles of the mandible. The trigeminal is therefore a mixed nerve.

VI. Abducent.—The abducent is a motor nerve which arises from the floor of the medulla and enters the orbit to supply the external rectus muscle of the eye.

VII. Facial.—The facial arises in close proximity to the Vth in the facialis ganglion. The ganglion is connected to the medulla, and distally it divides into an ophthalmic branch which unites with V^1, a large hyomandibular branch, a palatine and inner and outer buccal branches. It is primarily the nerve of the spiracle. The large hyomandibular passes outwards over the hyomandibular cartilage, and when it approaches the lower jaw it gives off, just under the spiracle, (1) two small branches to the inner aspect of the lower jaw which represent the chorda tympani of higher Craniates, and (2) its primary branch to the hyoid muscles. It shortly after splits up into numerous fibres which are distributed to the sensory canals of the hyoid and mandibular regions. The palatine branch is directed to the front of the spiracle, to which a prespiracular branch is given off, and it passes forwards to supply the mouth epithelium, ending in taste buds. The ophthalmic supplies the sensory canals of the front of the head, the outer buccalis those of the nasal region, and the inner buccalis the inner buccal sensory canals. The nerve is sensory, being related to the sensory canals of the head region and to sensory cells of the mouth and spiracle, and it is also motor in connexion with the hyoid musculature.

VIII. Auditory.—This nerve is sensory and originates in the auditory ganglion, the fibres being directed on the one hand into the medulla and on the other into the vestibule and ampullae of the auditory organ.

IX. Glossopharyngeal.—The IXth nerve arises in a ganglion

and is connected with the medulla behind the auditory nerve, and after passing through the hinder part of the auditory capsule the nerve is distributed to the first branchial cleft and the pharynx. It is a mixed nerve.

X. Vagus.—The vagus ganglion is connected to the wall of the medulla by several roots. Its nerve passes through the auditory capsule behind the glossopharyngeal. It divides into two branches: (1) giving off branches which bifurcate to supply the last four branchial clefts and then passes downwards to supply the heart and stomach; (2) the lateral branch, which is the nerve of the lateral line and is directed posteriorly along the dorsal wall of the body to reach the lateral epidermis of the tail.

The spinal cord gives off numerous spinal nerves which are segmentally arranged in pairs. The nerves result from the union of dorsal and ventral roots after these roots have passed out from the neural canal. The dorsal roots are ganglionated and sensory, and the ventral roots are simple and motor. The large pectoral fin is innervated by a fusion of the anterior spinal nerves, forming the brachial plexus.

The sympathetic system originates from the spinal ganglia and consists of a ganglionated cord lying just below and lateral to the vertebral column, the ganglia being connected with the spinal nerves by rami communicantes.

Sense organs are developed with relation to the brain and act as distant receptors.

The nasal organs consist of two sacs which are open below and are in the skate and many other Elasmobranchs connected by a groove each with the mouth. Each organ arises as an ectodermal involution, and the nerve in connexion with the involution as a ganglion. The epithelium is greatly increased in area, and the cavity interrupted by folds. The sensory cells are brought into contact with the water which enters the chamber and convey impressions of what answers in water to the olfactory function of air-breathers, a chemical stimulation of dissolved substances. The function is related to taste, as is that of the sensory canals of the skin.

The eye presents the typical craniate structure. It arises in the paired optic cups which are outgrowths of the

forebrain, and in the development of accessory structures. The cup comes into contact with the skin and is folded inwards. The skin ectoderm opposite the cup thickens and forms the lens. The cup by growth and a continuation of the involution is converted into two layers closely adposed, with the opening directed outwards. The inner forms the retina and the outer the pigment layer of the retina. The cup and the lens are enclosed in a double capsule derived from mesoderm. The inner is the choroid coat, which, like the retina, ends externally in a margin. The space defined by the margin is called the pupil. The margin forms the iris, and dorsally it is

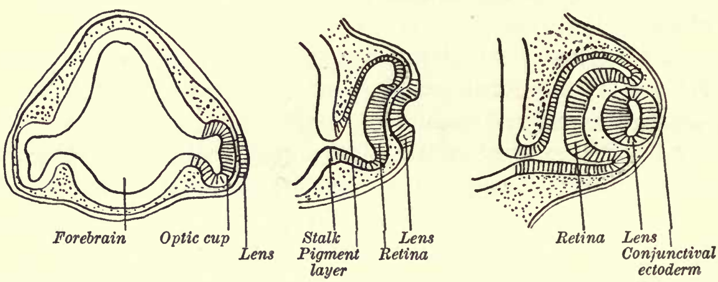


FIG. 90.—Torpedo. Development of eye. After Froriep.

folded to form a series of processes. The sclerotic is cartilaginous and completely surrounds the other structures. Opposite the iris and lens it is transparent, and this part of the sclerotic is termed the cornea. It is covered by a thin transparent conjunctiva continuous with the skin. The mesoderm enclosed by the retinal cup is converted into a transparent vitreous humour of gelatinous consistency, and the space between the lens and the cornea is filled with a watery fluid called the aqueous humour. The retina develops the sensory receptor rods and cones and nerve cells and fibres associated with them. The fibres are assembled to form the optic nerve, which leaves the eye through the stalk which connects the retinal cup with the thalamencephalon. The nerve therefore pierces the choroid and the sclerotic coats. The movements of the eye in the orbit are produced by the muscles mentioned above, and the eye is supported on a cartilaginous

peduncle which is articulated to the skull and to the eye by a knob-like projection of the sclerotic. As in all Craniates, the rods and cones of the retina lie close to the pigment layer; that is to say, the rays of light have to pass through the nervous layers to reach them. This goes to show that the retinal patch was originally external or developed directly by a pouch-like invagination of the ectoderm. In the Craniates the patch is developed from the forebrain, and its genesis can be seen even before the folding up is accomplished. It still develops the retinal elements on its original external surface. The eyes are, as in the higher Craniates, the organs of vision and, as in aquatic

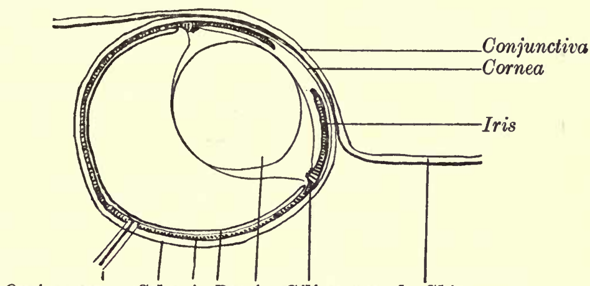


Fig. 91.—Raia. Diagrammatic vertical section of eye.

Craniates universally, the lens is characteristically spherical. In fishes the eyes enjoy a remarkable independence of movement, one eye remaining at rest while the other follows the movements of the object watched.

The auditory organ is developed from the ectoderm, the ganglion and the organ arising in close association. The thickening of the ectoderm deepens to form a paired cup which expands into a large sac connected by a narrow tube with the ectoderm, and lying one on each side of the rhombencephalon (fig. 79). The sac is then modified to form flattened regions mutually at right angles and all communicating with the remaining wide part of the vesicle. The compression continues until the cavity in each of the three areas is reduced to a marginal canal. Ultimately the parts of the compressed areas which intervene between the canals and the chamber below

are absorbed and the condition of the adult organ is reached. The organ comes to be lodged in a cartilaginous capsule, and it consists of a vestibule, the wide part of the original invagination still connected with the skin by a ductus endolymphaticus, and three semicircular canals. The canals are each dilated at one end into an ampulla. The posterior canal is peculiar in the skate in that it is circular and communicates with the vestibule by a small opening on its inner face. The vestibule and the small expansion called the utriculus, which receives the outer ends of the anterior and horizontal canals, contain

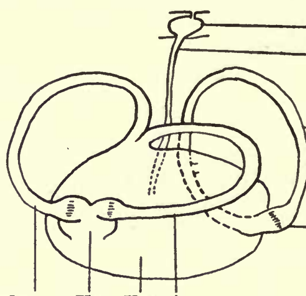


FIG. 92.—Raia. Auditory organ.

soft otoliths which entangle and are supported by the sensory processes of the cells of these parts of the organ. The ampullae similarly are provided with sensory cells, the processes of which support a gelatinous secretion. The canals are concerned by the flowing of the fluid or endolymph in conveying impressions of changes in position and equilibrium, but there is no doubt that the organ is also able to receive and transmit wave movements ; in other words, wave movements which correspond in water to the air movements or sound waves in terrestrial conditions. The endolymph is put into movement, and the movements are communicated by the movements of the otoliths to the sensory processes.

The auditory organ is a special organ associated with what is called the lateral line system, here in the skate mainly represented by the system of sensory canals, and the system is

connected with the VIIth and Xth nerves. These are brought into relationship with the VIIIth in the acoustic centre of the medulla and act as distant receptors of movements of the water. They are characterised by the secretion of mucus and have been found to be allied to taste in function, and the presence of the mucin gives rise to the impression that the organs may act as receptors also of electrical waves produced by the movements of living bodies even at a distance.

This is only a rough sketch of the complicated architecture of the nervous system and the associated organs for making it more perfect. It is as much as the student can be expected to make out by dissection and by the inspection of preparations. It is important to note that the morphology of the nervous system described above, which at once springs into place with the advent of the Craniates, is preserved in essentials in all. A due appreciation of the nature of the apparatus as a whole may be obtained by considering its general structure.

The motor roots of the spinal cord are related to the muscles derived from the myotomes. In the embryo the myotomes do not end at the anterior end of the vertebral column. We know that they are present in the posterior part of the skull, and we have good reason for believing that the parachordal mesoderm is derived from myotomes which either are not marked as such or have a fleeting history. With relation to the myotomes of the posterior part of the skull, which are apparent for a long period during development, ventral roots exactly similar to those of the spinal cord are formed. These undergo repression, both the myotomes and the roots, in front; but the survivors give rise to the muscles of the tongue, or the corresponding muscles and the roots form the nerve of these muscles, the XIIth or hypoglossal. These are duly developed in the skate and its allies, but are lost. In front of the hypoglossal region two other ventral motor roots are developed in similar manner, the VIth and the IIIrd, and these together with the dorsal IVth are directed to the innervation of the eye muscles.

These muscles are late in appearance relatively, and are developed from the mesoderm of the walls of certain cavities which appear in the mesoderm and which are also late in

development. The first of the series is the premandibular cavity and is independent, but the cavities on each side are connected by a canal, and this canal comes into close union with the hypophysis and the anterior end of the notochord. From their position in front of the alimentary canal and their attachment to the hypophysis, it is supposed that they are homologous with the head cavities of Amphioxus. The rest are serially repeated in continuation with the other divisions of the coelom, which extend between the gill slits and expand below into the pericardium or the forward part of the splanchnocoel. They are independent above, therefore, but are continuous below. They are called in succession the mandibular, hyoid, and first, and so on, branchial cavities. The premandibular yields the oculomotor muscles; the mandibular, the superior oblique muscle; and the hyoid, the external rectus. The remaining cavities are associated with the development of the visceral muscles of the arches. For some reason a desire has been exhibited to look upon the first three cavities as head somites; but without regarding them as somites, it could be argued that the mesoderm which gives rise to the muscle of the eye is derived from the anterior myotome mesoderm of the head. But there is no difficulty in regarding such muscles as being splanchnocoel in origin, for after all one of them at least is related to a nerve (IV) which cannot be regarded as a ventral root, but more probably as the motor survivor of a mixed dorsal root.

With these exceptions the cranial nerves are (1) purely sensory, I, II, and VIII; (2) mixed, V, VII, IX, and X, and like the dorsal nerves of Amphioxus they are situated between the somites and pass outside the somites. These visceral nerves of the head are derived from the neural crest and establish a second union with the skin just above the visceral cleft, forming what is called in each case an epibranchial ganglion. The neural crest is continued behind the Xth and survives in higher Craniates as the accessory or XIth nerve, which is motor. This crest also gives off internally small transient dorsal roots homologous with the spinal dorsal roots and corresponding to the hypoglossal roots below them. We have now good reasons for knowing that the spinal dorsal

roots and the mixed nerves of the brain are not homologous structures and may indeed coexist in the same segment. The spinal dorsal roots, moreover, lie medial to the myotomes. On the other hand, the cranial system of ganglia is carried back as the lateral line system as it is forwards by the ophthalmic, VII. As we have seen, this system is with the auditory an intimately related system, the acustico-lateralis system of special cutaneous sense organs.

From such studies we see that, in addition to segmental and primitive relationships, associations of function have taken place longitudinally, and we can thus resolve the nerves and their endings in the brain into groups :

- Sensory
  - Somatic
    - Special Cutaneous, I, II.
    - Acustico-lateral, VII, VIII, X.
    - General Cutaneous, V, IX, X, dorsal spinal.
  - Visceral
    - Taste, VII, IX, X.
    - General, VII, IX, X, dorsal spinal.
- Motor
  - Somatic, XII, ventral spinal.
  - Visceral, III, IV, V, VI, VII, IX, X, XI.
  - Sympathetic.
  - Secretory.

The **urinogenital organs** arise together in the coelomic mesoderm, and the system is peculiar to the Craniata.

The coelom is resolved into the dorsal segmented myocoel and the ventral unsegmented splanchnocoel. They remain connected for a period by narrow ducts which, like the myotomes above, are segmental. From the third myotome behind the head and extending backwards in succession this connecting tube is the seat of formation of a primitive kidney tube, and it has consequently been called the nephrotome (fig. 85).

The upper part of the nephrotome is concerned in the development of the sclerotome, and this is separated at the time that the nephrotome loses its connexion with the myotome.

The nephrotome remains connected with the splanchnocoel, and its parietal wall expands into a swelling. In the Elasmobranch fishes the anterior part of the kidney does not become functional, and the nephrotome and the swelling are at first without a cavity. The same changes take place in the succeeding four to seven segments, and the outgrowths of the nephrotomes fuse to form a single mass, the pronephros. The outer part of the mass forms a duct and it extends posteriorly and fuses with the terminal end of the intestine. This is the

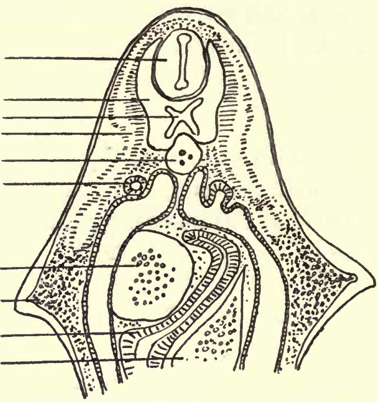


FIG. 93.—Transverse section through region of anterior end of pronephric duct of embryo of Acanthias.

pronephric duct. In typical conditions the pronephric tubules possess a cavity which opens in each case into the dorsal angle of the splanchnocoel, and this opening is called a nephrostome; this state of the pronephros is retained in the lowliest Craniates, the lampreys and hags. The blood, moreover, in such comes into close association with expansions of the tubules forming a glomerulus.

The pronephros is a larval kidney and it will be seen that it is altogether different in origin and structure from that of Amphioxus. It is derived from the coelom and is discharged by a coelomiduct.

The pronephros is succeeded by another series of tubules formed in precisely the same fashion, but, as is plain, the

outgrowth of the nephrotome in their case has to establish an opening into the pronephric duct. A large number of segmental tubules are formed in this way and successively connected with the pronephric duct. This second set of tubules constitutes the mesonephros.

Each tubule is connected to the splanchnocoel by a nephrostome or peritoneal funnel, and the other end opens into the pronephric duct. Between these two openings the tube expands to form a Bowman's capsule, and the capsule is indented by a glomerulus and thus a Malpighian body is produced.

The segmental tubules, to begin with, are small and gradually gain in size and functional importance posteriorly. In the female, moreover, the first seven to nine mesonephric tubules are rudimentary. In the male they persist to take part in the formation of the vasa efferentia.

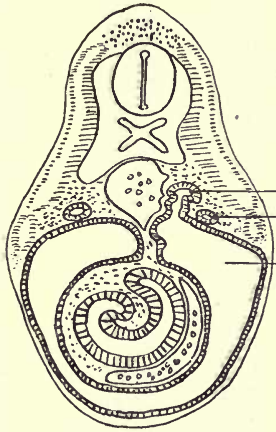


Fig. 94.—Transverse section through mesonephros of embryo of Acanthias.

In association with sex, moreover, a change takes place which converts the pronephric duct into male and female gonoducts. In the female, one of the pronephric nephrostomes expands, while the rest are atrophied and disappear. This persisting opening forms the inner opening of the oviduct or Müllerian duct. Then further back the pronephric duct where it is associated with mesonephric tubules is split off longitudinally, and the longitudinal division goes on posteriorly so as to remove the part of the original duct connected with the tubules from the part communicating in front with the persisting opening of the pronephros. The duct is therefore divided into an oviduct and a mesonephric duct.

In the male the two ducts are similarly divided, but the anterior seven to nine mesonephric tubules are connected to

the testis, and thus the mesonephric duct is in the male also a vas deferens.

As growth proceeds the anterior mesonephric tubules are gradually reduced, except those which in the male form the

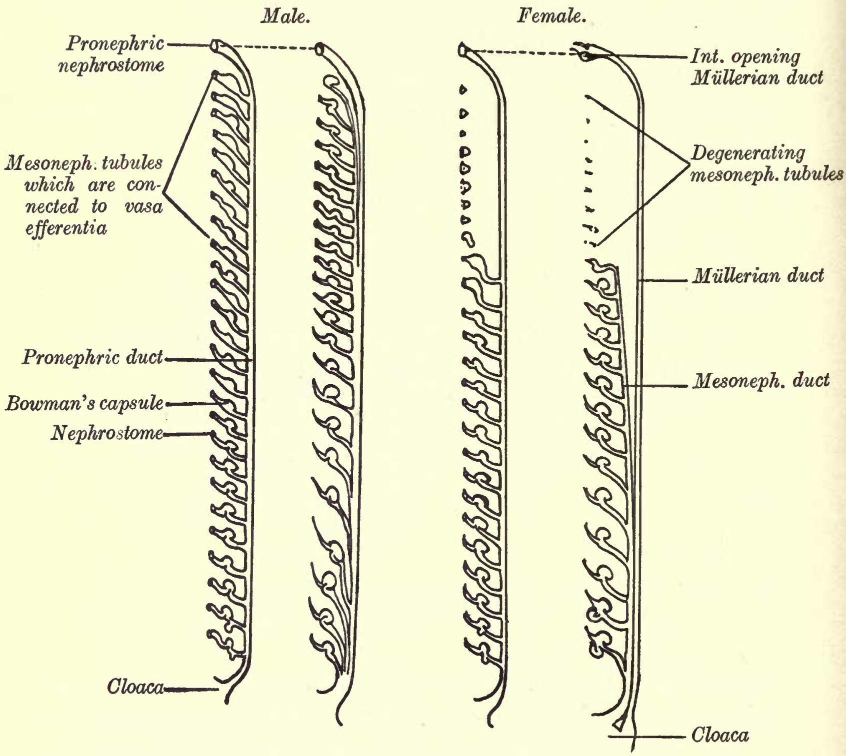


FIG. 95.—Diagram of mesonephros of male and female Pristiurus. After Rabl.

vasa efferentia and the mesonephric duct which functions as a vas deferens. The posterior tubules are directed more and more backwards before fusing with the mesonephric duct, and ultimately the functional kidney part of the mesonephros is separated by a duct or ducts, the ureter or ureters, connected only with the mesonephric duct at its termination.

The germ cells appear over a great part of the same area as the pronephros and the mesonephros. They are

segmentally arranged to begin with, but the ridge they form on each side, the genital ridge of the peritoneum, suffers a reduction and concentration.

This introduction will serve to make plain the condition of the adult organs.

The spermatozoa are liberated into tubes in the testes of the male, and these tubes open into the anterior tubes of the mesonephros and are the vasa efferentia, which fuse to form a

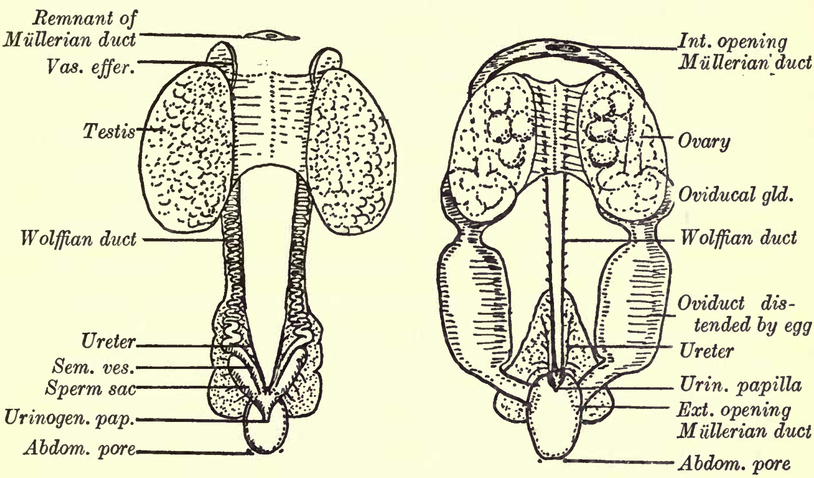


FIG. 96.—Raia. Male (left) and female (right) reproductive organs of adult.

marginal duct leading into the mesonephric duct or Wolffian duct. The duct is highly convoluted and forms a compact organ extending almost the length of the peritoneal cavity. This organ is called the epididymis, or Wolffian body. The two vasa deferentia as they emerge from the epididymis become dilated to form seminal vesicles and give off blind sperm sacs. They join to form a urinogenital sinus with the ureters from the kidney or functional part of the mesonephros. The sinus opens by a papilla which projects into the cloaca from the dorsal wall. The kidneys are large, red in colour, and lie one on each side of the vertebral column at the hinder end of the peritoneal cavity.

In the female the large ova, which are light yellow in colour,

are shed into the peritoneal cavity. They enter the common anterior end of the oviducts or Müllerian ducts, the paired openings described above having merged to form a single opening. The oviducts are well developed and have separated completely from the mesonephric duct. They open separately into the cloaca on each side. The kidney is placed as in the male, but the ureters on each side open into a urinary sinus and the latter into the cloaca by a urinary papilla. The remains of the primitive mesonephric duct may be traced forwards as two fine tubes from the urinary sinus. Moreover, in the male a vestigial remnant of the anterior end of the oviduct occurs on the ventral aspect of the oesophagus.

Development.—The eggs are very large in all Elasmobranch fishes. The cytoplasm is distended with yolk to a degree similar to that of birds, and the nucleus is left at the animal pole as a very small element in a very large cell. In the case of the ovum of Acanthias taken from the ovary the nucleus was calculated to be only $\frac{1}{4000000}$th of the bulk of the ovum. The egg is protected by two membranes. The outer appears to be derived from the follicular cells and would therefore be called a chorion. The inner is secreted by the cytoplasm of the egg and is therefore a vitelline membrane. When the egg is ripe it is burst from the follicle into the peritoneal cavity and it is carried forwards to the internal opening of the oviduct. In the upper part of the oviduct the ripening process is finished and the two polar bodies are placed outside the cytoplasm at the animal pole. Spermatozoa gain entrance, and one of the male pronuclei fuses with the female pronucleus. The rest are relegated to the side, ultimately disappearing. The spermatozoa are long and flagellate, with elongated heads.

The glands in the upper part of the oviduct secrete albumen which is coated over the egg, and the egg is then conducted through the oviducal gland, where a horny case is secreted, and this completes the envelopes.

As in the case of the bird, therefore, the egg is protected by envelopes developed in the ovary, and secondarily by albuminous and shell coverings by the glands of the oviduct. The albumen and the horny case are little developed or absent

in viviparous Elasmobranchs, but they are well developed in the skate and other oviparous forms.

The horny case varies in shape according to the species. In the skate and its allies it is a depressed rectangular case, flat on one side and rounded on the other, and the corners are drawn out into stiff, bent, tubular processes open at the end. When the eggs are deposited these serve to anchor the eggs to stones and zoophytes at the bottom of the sea, and to produce currents of water of respiratory service. When development is completed after some months' incubation the young skate emerges from an opening at one end.

The segmentation of such a large ovum is necessarily confined to the animal pole. The microscopical segmentation nucleus divides, and the division is followed by a superficial incision of the cytoplasm separating the two nuclei. The yolk is altogether unaffected. Such a segmentation is called meroblastic. As segmentation proceeds a mass of cells appears at the animal pole, and this is called the blastoderm. Superficially it has the appearance of a round patch of cells in which the central elements are small and the peripheral next the yolk rather larger. In section the patch proves to be several layers of cells deep. A blastula is thus formed, and in some Elasmobranchs the segmentation of the animal pole is followed by late and partial indication of segmentation affecting to a slight extent the yolk immediately outside the area.

The conversion of such a blastula into a gastrula by an invagination of the yolk is obviously impossible, and in spite of the long history of invagination a return to delamination is made. The cells of the blastoderm, or blastomeres, are resolved into ectoderm and endoderm, the former external and the latter internal next the yolk, and both are continuous at the margin, which now becomes the mouth of the blastopore. A segmentation cavity is also developed between them in the process.

The middle of the flattened ectoderm marks the anterior end of the embryo, and the dorsal lip of the blastopore at once becomes evident as the primitive posterior end; and between these two points, to begin with, the neural plate is formed, all of which is destined to form the anterior part of the brain.

The dorsal lip during its backward growth continues to yield a continuation of the ectoderm and the endoderm, the former extending the neural plate, and the latter, notochord and coelomic mesoderm. But while it is growing and its products being converted into these structures the rest of the blastopore is enveloping the yolk in ectoderm and endoderm. Not only

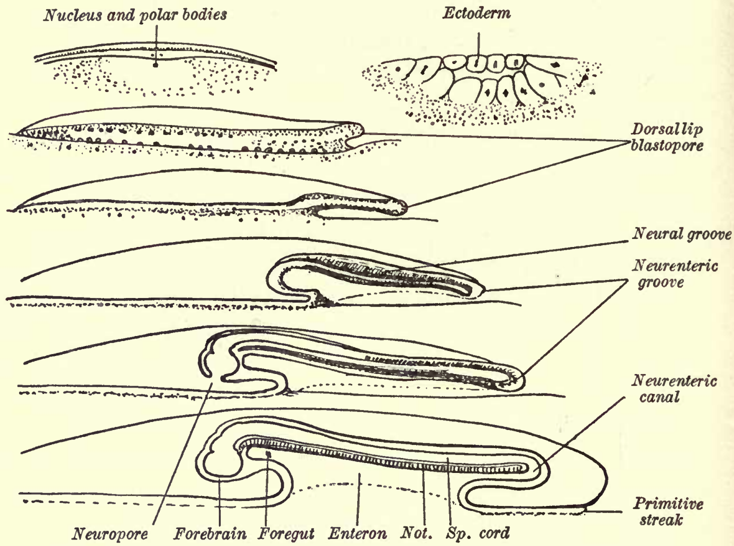


FIG. 97.—A succession of diagrammatic longitudinal sections to illustrate the development of Elasmobranchs.

so, but the margin is also producing a mesoderm which forms the mesenchyme of the yolk between the ectoderm and the endoderm. A continuous mesoderm is thus formed, but it is most pronounced at the dorsal lip and on each side of it. The gastrula therefore passes at once into the postgastrula condition.

The growth at the posterior end raises the margin of the blastopore from the yolk. A cavity is thereby formed medianly and posteriorly, separating the endoderm from the yolk, and the excavation extends into the primitive gastral region, to the anterior end of the embryo. This end of the embryo at

the same time is raised from the blastoderm as the head fold, and the fold marks permanently the anterior end of the embryo. Both layers are raised, and the growth of the fold extends forwards and upwards. Thus a pouch of the endoderm is produced as the anterior end of the enteron. The embryonic region between the head fold and the dorsal lip becomes thereafter more pronounced by the flattening and grooving of the ectoderm in the formation of the brain, and by a corresponding flattening of the endoderm below in the formation of the anterior end of the notochord. Sections show also that the coelomic mesoderm is being budded off from the edge of the flattened notochord.

Growth is accelerated laterally in the region of the embryo, forming and raising the ridges defining the neural groove, and the growth extends to the posterior margin, where the two ridges are continued into two prominences defining between them a neurenteric groove.

The medullary or neural groove is gradually raised and fused, being converted into the neural canal. The canal remains open for some time as a neuropore in front.

At the posterior end of the embryo the groove remains open until the time comes for the conversion of the neurenteric groove into the neurenteric canal. This is done by the rotation ventrally of the prominences and their fusion all round the posterior end of the embryo. The fusion forms a tail fold containing a posterior portion of the enteron communicating by the neurenteric canal with the neural canal. The line of fusion is the median line of the embryo, and the fusion is continued below over the yolk, where the line of fusion of the lips of the blastopore forms a primitive streak.

There is a great deal of this which is similar to Amphioxus. It is to be observed, however, that the fusion which produces the neurenteric canal in Amphioxus completely obliterates the blastopore, but in the Elasmobranchs it is only the upper or dorsal part of the blastopore which is so converted. The rest of the blastopore forms a line of fusion of ectoderm and endoderm extending beyond the embryo. In both cases we have an embryo the enteron of which is extended into the neural canal and opens anteriorly by a neuropore. It is

covered externally by ectoderm, for we may now presume that the ectoderm has advanced completely over the yolk. The endoderm presents on its roof the notochord, which is narrowed and separated. With the formation of the neurenteric canal the growth of the nerve cord, of the notochord, of the mesoderm, as of the covering ectoderm and the enteric endoderm, proceeds directly from the cells, constantly multiplying in the neighbourhood of the neurenteric canal.

The fate of these structures has already been pointed out in the foregoing account. It will be plain that as the embryo increases in size the yolk appears smaller in comparison, forming a sac depending from the ventral side of the embryo. It is called the yolk sac, and the attachment to the body, which is narrowed, is called the umbilical cord. Finally, its contents are completely absorbed and the sac disappears, the ectoderm merging in the ectoderm of the body at the point of attachment, and the endoderm in the intestinal wall.

At an early period of the embryonic life the gills are produced into long filaments or external gills, the hyoid and the other gills contributing to form a large number of long filamentous external gills. They remain until the time of hatching approaches, when they are gradually atrophied.

CHAPTER X

AMPHIBIA

Phylum VERTEBRATA	
Sub-Phylum CRANIATA	*Type*
Class AMPHIBIA	Rana

THE common frog, *Rana temporaria,* is widely distributed over the northern hemisphere, and it is common in the British Isles. The edible frog, *Rana esculenta,* extends from southern England through Europe to the African side of the Mediterranean and to Japan. The genus is mainly a northern one, but it is cosmopolitan, and about a hundred species have been described.

The common frog is common on moors and in damp situations. The adult is terrestrial usually, retiring in habit, avoiding capture by its characteristic jumping so as to gain a place of hiding in the grass. In the winter it hibernates in the soil under roots of shrubs, moss, and the like, or at the bottom of a pond. In the spring it migrates to fresh water for spawning purposes. The floating egg-masses of the species of Rana, Bufo, and other genera, are well known. The young escape from the eggs as tadpoles, pass through a metamorphosis and a period of growth to the adult. Maturity is reached in about three to four years. The first winter may be passed as a tadpole, but usually as a young frog.

The food, to begin with, is a plant one, but speedily becomes animal, and after metamorphosis may be said to be purely animal. Insects form the main diet, but molluscs, worms, and crustaceans are utilised as well. The food is captured when it is moving, the frog jumping to reach it, at the

same time launching the tongue, which is the instrument of capture.

The enemies of frogs are many, and range from insect larvae and fishes in the water to snakes and birds on land and in water, but man makes a great demand on frogs. Species of Rana are used for food on the continent of Europe (*R. esculenta*) and in America (several species), and large numbers are employed in zoological and physiological laboratories.[1]

External Characters.—*Rana temporaria* is distinguished by the black patch behind the eye. The colour generally is yellow or brown with patches of brown or black, and it is variable and under control. The skin is smooth and moist. There is no skeleton associated with the skin, but such is developed in the South American Ceratophrys.

The head is broad and flat and passes into the body without a neck, and there is no tail. The anterior limbs are short, and the digits are not webbed. The posterior limbs are long, and the toes are connected by a web. The hand of the male bears on its inner aspect a swelling which expands in the breeding season into a dark brown glandular cushion for clasping the female.

On the dorsal aspect of the head there will be seen the paired nasal openings, the prominent eyes, each with a thick upper and a membranous lower eyelid, and the rounded area in the black patch, which is the tympanum of the ear—there is no external ear or outer passage. The mouth is a wide opening occupying the margin of the head, and if it be opened and distended several important features of structure are brought into view. The margin of the upper jaw is formed by the premaxillae and the maxillae, which bear a row of small pointed teeth. So also do the vomers, which lie immediately behind the premaxillae. Just externally to the vomers the roof of the mouth presents the inner openings of the nasal passages, which thus extend almost directly from the surface of the head into the roof of the mouth. In other words, the nasal passages are not carried backwards with the formation of a palate. The centre of the roof of the mouth is occupied

[1] 1920. Wright, *Frogs, their Natural History and Utilisation.* U.S. Fish. Bur. Doc. No. 888.

by the narrow floor of the brain case, and on each side of this the roof is membranous under the orbits. Behind this region the roof passes into two large passages which lead each into the chamber bounded externally by the tympanum. This chamber is the middle ear, and the wide passage leading into it from the mouth is the Eustachian tube.

The floor is bounded by the lower jaw, or mandible, which does not bear teeth. The tongue occupies the middle of the floor, to which it is attached anteriorly and projects freely backwards. The anterior end is rounded, the posterior end is forked. The tongue, as has been said, is used in the prehension of food, and can be shot out from the mouth and retracted with the prey with such rapidity that the eye fails to observe the movement. The adhesiveness is provided by intermaxillary glands at the anterior end of the roof of the mouth, glands against which the tongue brushes as it is being launched. Beyond the tongue the longitudinal opening of the glottis may be made out, and also that the cavity narrows to form the oesophagus.

The limbs are resolved into segments which may be defined as anterior—arm, forearm, hand; posterior—thigh, leg, foot. An extra segment is provided in the posterior limb by the elongation of the tarsus, or ankle, a feature associated with the jumping powers.

The hinder opening common to the intestine and the urinogenital organs is the cloaca, situated at the end of the body, between the hind limbs.

Internal Structure.—The **skeleton** is founded on cartilage, but is to a large extent a bony one. Many of the bones replace the cartilage more or less completely, but some of the bones are developed independently of the cartilage. In the case of the replacing bones the cartilage degenerates, and the space it occupied is invaded by bony formation. The independent bones are formed directly by the connective tissue of the region being converted into bone. In both cases the procedure is essentially the same. Heralded by a calcification usually, a layer is developed, the periosteum, which divides, and the cells are separated by a connective-tissue matrix containing gelatin and which becomes hardened by lime salts.

Bone expands by growth of the periosteal layer, successive layers being formed. The skeleton thus gains in hardness and in rigidity, but it loses in elasticity.

The vertebral column is formed around the notochord of the larva. Cartilaginous arches are developed in the mesoderm around the notochord and spinal cord, those on the dorsal side being conspicuously large. The latter expand upwards to form the neural arches. Along the notochord a series of chondrifications of the sheath of the notochord form a series of intersegmental rings. A split appears in each ring separating the centra; and in the middle of each centrum cartilage is formed in the notochord. A ring of bone appears early in each centrum, and the cartilage is gradually replaced by bone. The haemal arches become more conspicuous posteriorly.

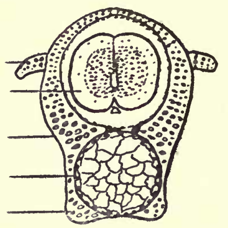


FIG. 98.—Development of vertebra. Cartilaginous neural and haemal arches fusing to form neural arch and centrum.

All the figures in this chapter refer to *Rana temporaria*.

In the frog there are nine vertebrae and the urostyle.

The second to the seventh vertebrae are formed in each case of a flattened centum bearing a neural arch and produced laterally into the prominent transverse processes. The arch extends upwards into a small spine, and anteriorly and posteriorly bears articular processes, or zygapophyses. The articulation is, as usual, the posterior processes overlapping the anterior of the succeeding vertebrae. Each of these vertebrae is procoelous; that is to say, is hollow in front and rounded behind. The first vertebra differs in the absence of transverse processes and anterior articular processes. It is attached to the occipital condyles of the skull by two diverging facets on its anterior surface. The eighth is amphicoelous—hollow at both ends of the centrum. The ninth forms the sacrum, and is at once distinguished by the stronger upwardly directed transverse processes, which are articulated to the ilia of the pelvis. The centrum is convex in front and presents two projecting processes behind for the articulation of the urostyle. The

urostyle is the long median bone which continues the vertebral column to a point just in front of the cloaca, where it ends in cartilage. The urostyle receives the posterior end of the spinal cord and presents anteriorly a pair of openings for the passage of the last pair of spinal nerves. It is the result of the fusion of the anterior caudal vertebrae, but it is formed of a single mass of cartilage, mainly contributed by the ventral arches (fig. 104).

When the vertebral column is viewed in the articulated condition it will be seen that there is a series of intervertebral foramina for the passage of the spinal nerves.

The skull is formed upon a cartilaginous basis. The parachordals are developed on each side of the anterior

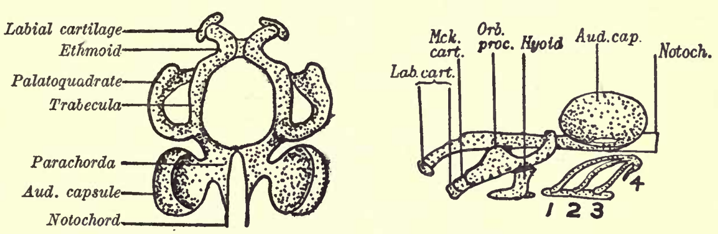


Fig. 99.—Cartilaginous skull of young tadpole from above, and from the side. After Marshall.

end of the notochord. The trabeculae are widely separated, but posteriorly they approximate to meet and fuse with the parachordals, and anteriorly to form the ethmoid region. Here also they form cornua, below which are produced a pair of labial cartilages, and corresponding labial cartilages appear below in the floor of the mouth.

The tadpole skull is a cartilaginous one developed from these elements which expand to form a brain case. It is produced to provide a capsule for the nose on each side in front, and it fuses with the auditory capsule posteriorly. The brain case is open above by large median and paired posterior fontanelles. The upper element of the mandibular arch, the palatoquadrate, is well developed in the form of an arch uniting the ethmoid region to the auditory capsules. It is produced into orbital, ascending and otic processes, and midway provides a surface for the articulation of the cartilage of

the lower jaw, Meckel's cartilage. The gills of the tadpole are associated with a hyobranchial cartilaginous skeleton.

About the period of metamorphosis changes take place which convert the tadpole chondrocranium into a condition approaching the adult.

The chondrocranium persists to a large extent, it is only partially replaced by bone. The sphenethmoid, or orbitosphenoid, is a ring-like bone which is developed around the brain case in the front region of the orbit. The exoccipitals, the only occipitals developed, replace the cartilage posteriorly on each side of the foramen magnum. The prootics replace a large part of the original auditory capsule. Another bone of great

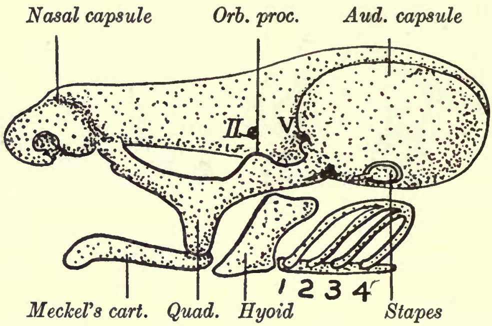


Fig. 100.—Cartilaginous skull of older tadpole from the side.

interest preceded in cartilage is the columella auris. In the adult this bone lies in the cavity of the middle ear, bridging the space between the tympanum and the fenestra ovalis. In the tadpole it arises in association with the auditory capsule. The lateral ventral aspect of the capsule remains unchondrified, and the membranous space thus left is the fenestra ovalis or fenestra vestibuli. It becomes narrowed and crescentic, and the median part of the crescent is cut off to form a plate-like cartilage occupying the membrane like a disc. This is the stapes. In front of the disc an independent chondrification of the fenestra gives rise to a rod-shaped cartilage which is the columella. This chondrification takes place in the roof of the cavity of the middle ear, which is the hyoid cleft and homologous with the spiracle of the fish, and extends in the

mesenchyme to the palatoquadrate. The palatoquadrate is soon after deflected and lengthened to occupy a position further back, and the columella is thereby brought into relationship with the membrane which forms the outer wall of the blind pouch of the hyoid cleft; and in this region a ring-like cartilage develops as the tympanic annulus, and it supports this membrane and the enclosed area of the skin which are now converted into the drum of the ear.

The other bones of the brain case are covering bones, developed, that is to say, independently of the cartilage. They

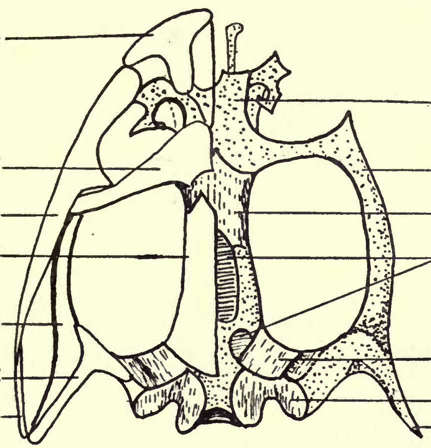


FIG. 101.—Dorsal view of frog's skull. The covering bones shown on the left are unshaded, the cartilage on the right is indicated by dots, and the 'cartilage' bones by broken lines.

are conveniently called membrane bones, although some of these bones may be the products of both processes. The membrane bones of the skull are early formed. They have to be removed to disclose the cartilaginous structures which they cover. This may be most readily accomplished by steeping the head of the frog in glycerin.

The roof of the skull is occupied by the triangular nasals and the fused fronto-parietals. The floor is protected by the dagger-shaped parasphenoid and the vomers. The premaxillae and the maxillae form, with a short quadrato-jugal or quadrato-maxilla, the outer arcade of the roof of the mouth; the palatines

and pterygoids, the inner arcade. The palatine lies transversely between the sphenethmoid and the maxilla and supports the nasals above. It gives articulation to the pterygoid, a long graceful bone resolved into three processes: an anterior, articulating with the palatine and abutting against the maxilla; an inner, articulated to the prootic; and a posterior, which extends to the posterior end of the upper jaw and supports the squamosal. The squamosal is a prominent T-shaped bone. The upper inner limb of the bone is articulated to the prootic,

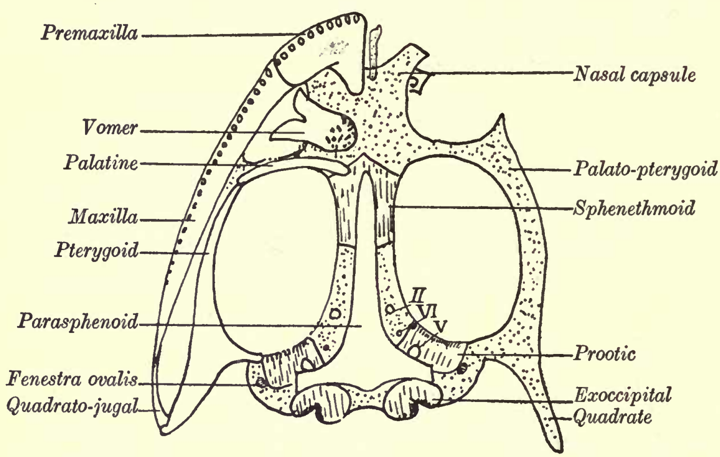


FIG. 102.—Ventral view of frog's skull. See explanation of fig. 101.

and the lower extends to the end of the upper jaw, where it covers the quadrate cartilage.

The lower jaw is developed around the mandibular or Meckel's cartilage and consists of an anterior dentary, which is, however, toothless, and a posterior angulo-splenial.

The columella auris is, from its method of appearance and its position, looked upon as a product of the upper part of the hyoid arch. The rest of the hyoid arch persists. Just below the fenestra ovalis the anterior cornu of the hyoid, the elongated hyoid arch, fuses with the auditory capsule, and the arch forms a graceful curve to reach the anterior face of the flat body of the hyoid bone. This bone is produced by the fusion of the basal elements of the larval hyoid and the

first branchial arch. The posterior cornua, which are articulated to it posteriorly and are directed backwards on each side of the glottis, are the modified ventral elements of the first branchial arch. All the rest of the branchial apparatus disappears.[1]

The limbs are developed as paired thickenings of the somatopleure mesoderm, and the girdles are developed first.

The rudiments of the anterior limbs up to the time of metamorphosis remain covered by the opercular fold. The mesodermal thickening grows upwards and downwards in

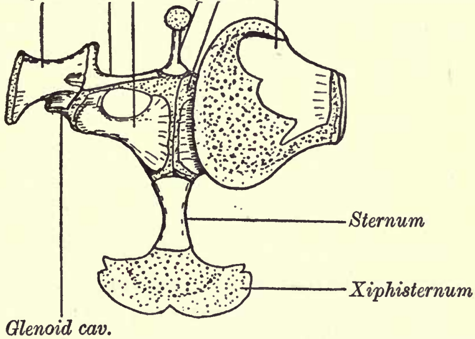


Fig. 103.—Pectoral girdle from above. After W. K. Parker.

the body wall and becomes chondrified. The upwardly directed part forms the scapula, and the lower is resolved into two processes—the precoracoid and the coracoid. The scapular portion divides into suprascapula and scapula; the former is partially and the latter completely ossified. The lower ends of the two coracoids fuse to form the epicoracoids, and in front and behind paired cartilaginous elements appear which fuse medianly. In front they form the epi- or omosternum, which is replaced by bone next the girdle, and posteriorly the elements become resolved into the bony sternum and the cartilaginous xiphisternum. A membrane bone is developed along the anterior border of the precoracoid, and

[1] 1897. Ridewood, *Proc. Zool. Soc.*

this is the clavicle. A glenoid cavity appears between the scapula and the coracoid and gives articulation to the humerus.

As the bud appears and lengthens, cartilages are formed in succession and are the precursors of the bony skeleton of the limb.

The humerus of the male possesses a highly developed deltoid crest. The radius and ulna are fused, and the ulna presents an olecranon process. The carpus consists of six small elements—a radiale and an ulnare, a centrale and three carpalia. Of these last, one each is related to the first and second metacarpals and the third to the remaining metacarpals ; it is formed by the fusion of the outer carpalia and includes also a centrale. There are five metacarpalia, but toes are developed only on II to V. The phalanges number 0, 2, 2, 3, 3. The second metacarpal is enlarged in the male to support the copulatory pad.

The hind limbs appear externally before metamorphosis in the frog, but the manner of development is essentially the same as that of the anterior limbs. The thickening of the somatopleure mesoderm extends upwards to form the ilium, and below to form the ischium and the small pubis. The ventral ends of the cartilaginous arches meet and fuse. The acetabular cavity appears near the ventral end of the arch, and the ilium and the ischium become ossified, the pubis remaining cartilaginous. At first the girdle is vertically disposed, but it is rotated backwards as the limb gains in length.

The pelvic girdle of the adult frog is catapult-shaped. The ilia are strongly developed as long processes which articulate at their anterior ends with the transverse processes of the sacral vertebra. Posteriorly they are fused. The rounded acetabular cavity is completed posteriorly by the fused ischia and below by the fused cartilaginous pubes. The three elements of the girdle thus meet in, and contribute to the formation of, the acetabulum.

The posterior limbs are made up of longer elements than the anterior limbs. These are, in succession, the femur, the fused tibia and fibula, the characteristically elongated astragulus and calcaneum of the tarsus which are fused

proximally and distally, the remaining two small elements of the tarsus, the five metatarsalia, and the phalanges. The phalanges number 2, 2, 3, 4, 3. There is in addition, on the medial aspect of the first toe, a small process called the calcar. This consists of a small metatarsal and one or two phalanges, and it is believed to be a prehallux, or additional toe, which has early in the phylogenesis of the Amphibia and their successors been discarded.

The skin is thin and tends to become resolved into a superficial horny layer of flat cells and a lower layer based on a Malpighian layer. The former is moulted periodically, the shedding beginning at metamorphosis and continuing during growth. The discarded stratum corneum is eaten. The

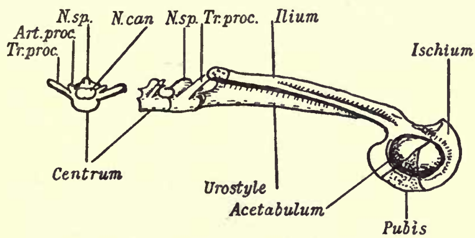


FIG. 104.—Pelvic girdle and posterior vertebrae from the side. An end view of a vertebra is given.

skin is beset with mucous glands, and in some frogs a special accumulation of glands is formed on each side dorsally, and these are called paratoid glands. The secretion of the paratoid glands of toads, newts, and salamanders is poisonous. The ectoderm is supported on a connective-tissue dermis bearing blood-vessels and nerves, and it is into this layer that the skin glands grow from the ectoderm. The skin, moreover, is to a large extent separated from the muscular wall of the body by large spaces containing lymph.

The **alimentary canal** is formed almost entirely of endoderm. The anterior ectodermal invagination, or stomodeum, contributes the front part of the mouth, and the posterior invagination, or proctodeum, the posterior part of the cloaca.

The general features of the mouth cavity have already been described. The mucous membrane of the mouth narrows

posteriorly to form the oesophagus, and almost immediately gradually expands into the elongated stomach. Both the oesophagus and the stomach present tubular glands. The stomach ends distally in a constriction which marks the position and the effect of the contraction of the sphincter muscle of the pylorus. The small intestine at its beginning is directed forwards at a slight angle with the stomach. This is the duodenum, and it receives the pancreatic-bile duct. The lining membrane of the distal part of the duodenum and

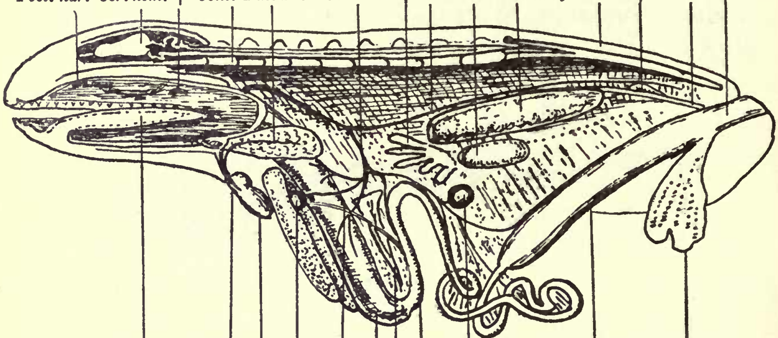


Fig. 105.—General dissection from the side.

a great part of the rest of the small intestine is produced into a series of posteriorly directed pocket valves, similar to the semilunar valves of the circulatory organs. The mucous membrane is much folded, and the cells secrete mucus. A sudden expansion of the intestine marks the beginning of the large intestine, and this is directed backwards and upwards to open into the cloaca.

The liver is developed from the outgrowth of a pit which is formed at an early period in the anterior part of the floor of the primitive enteron. In the adult the liver is resolved into right and left lobes, and it is incised into subsidiary lobes. The space between the two lobes is occupied by the green gall bladder. It will be observed that the bile duct commences

in the right lobe, is connected with the gall bladder by a cystic duct, and receives tributary ducts from the left lobe. As it runs down the mesentery between the duodenum and stomach, it passes through the pancreas and receives from the pancreas the pancreatic duct. In the lower part of its course the duct is therefore a pancreatic-bile duct, and this opens into the duodenum. The pancreas is the triangular yellow patch which occupies so large a portion of the mesentery, connecting the duodenum with the stomach. The digestive processes are very similar to those of the higher Craniata.

The **respiratory organs** of the adults are a pair of lungs which arise as paired outgrowths of the oesophageal wall. These meet to form the single opening, the glottis. The glottis opens into a larynx, and the larynx is supported by arytenoid cartilages developed with constrictor and dilator muscles from splanchnic mesoderm,[1] and the inner layer is reflected to form vocal cords. Frogs are silent usually, except in the breeding season, when croaking is indulged in. The lungs spring at once from the tube immediately below the larynx, and are delicate sacs lying one on each side of the oesophagus. The walls are protruded into shallow air sacs, and the thin epithelium of the air sacs and of the network of capillaries brings the blood into intimate relationship with the air. Breathing is accomplished by the floor of the mouth being depressed, with the result that air is drawn into the mouth cavity through the nasal passages. The valve in the nostril is closed and the air is driven into the lungs by the raising of the floor of the mouth. The respiratory pigment is haemoglobin, as in other Craniates.

The skin is also used for respiration, and when the animal is submerged is necessarily the organ of breathing.

Coelom.—The coelomic mesoderm is resolved into dorsal myocoels and the ventral splanchnocoel. The myocoels are segmented, and after they are separated from the splanchnocoel they lose their cavity and grow downwards. Their inner cells form the skeletal musculature and buds are developed from them to the limbs, and their outer layer is converted into the dermis. With the loss of the tail the primitive

[1] 1920. Edgeworth, *Jour. of Anat.* vol. 54.

segmental muscular system is practically lost. The muscles of the body and limbs become modified in such a way that homologies with the muscles of the higher Craniates are at once suggested, and, indeed, the nomenclature of human anatomy is used in describing them. This will be plain if, as soon as the frog is pinned out in the dissecting dish and the skin reflected from the ventral surface, a glance be given to the muscles of the body wall. The recti meet medianly in a linea alba and are interrupted by transverse lines of connective tissue. Lateral to them are the internal and the external oblique muscles. In front the large pectoralis muscles are prominent, and the myohyoid muscle which occupies the floor of the mouth. The upper segments of the hinder limbs are very muscular, and the muscles are defined by names familiar to the medical student.

The cavity of the splanchnocoel gradually extends ventralwards, and in doing so separates the mesoderm into parietal and visceral layers. The body cavity thus formed is resolved into the forward pericardium and the posterior pleuro-peritoneal cavity. As soon as the body wall is cut through, the muscular layers being noted and the abdominal vein isolated, the pigmented peritoneum is seen as a membrane which lines the body cavity and which is reflected dorsally to support and cover the viscera. It is a closed cavity completely lining the internal surface of the body wall, and reflected in two layers dorsally to form the mesentery, which diverge to receive the alimentary canal and other viscera. Anteriorly it is reflected to form a covering for each of the lungs, a visceral pleura thus being produced, and it comes here into contact with the pericardium. In the female the peritoneum is pierced anteriorly by the internal openings of the oviduct. The pericardium is also a closed sac, so disposed that the inner or visceral layer is closely attached to the heart, and that anteriorly it is reflected to form the parietal layer, which also completely envelops the heart. These membranes provide smooth moist adposed surfaces externally to the viscera, and thus the movements of the latter are facilitated.

The myocoel develops a sclerotome which yields mesenchyme to ensheath the notochord and the nerve cord, and it is

in this mesenchyme that the skeleton of the vertebral column is developed.

Vascular System.—The mesoderm also yields a general mesenchyme in which the blood and blood-vessels and the lymph and lymph-vessels form. It is said by some investigators that the heart is formed from yolk cells—that is to say, directly from endoderm ; and Schwink explained the appearance as being due to a delamination of the yolk cells into endoderm and mesoderm. From a consideration of the happenings in bony fishes, it is probable that the mesenchyme of the heart, which is enclosed by the primitive pericardium, is due to wandering cells of the mesenchyme.

In the adult frog the blood consists of a clear plasma which bears oval flat nucleated erythrocytes containing the haemoglobin, together with leucocytes and thrombocytes. The latter are active in producing thrombin, and so fibrin, in the plasma in coagulation.

The blood is brought to the heart by the three caval veins. These combine to form the triangular-shaped sinus venosus on the dorsal side of the heart. From the sinus venosus it is propelled into the thin-walled right auricle through the sinu-auricular opening, which is guarded by two valves. A smaller left auricle receives the blood from the lungs at the same time by the pulmonary veins, which join to form a small aperture in the dorsal wall of the left auricle. Both the auricles contract next, and the blood is sent into the single ventricle. Two valves guard the opening common to the two auricles, and the septum which separates the auricles is continued on to their anterior surfaces. The valves are attached to the walls of the ventricle by deep folds which may be regarded as incipient chordae tendineae. The walls of the ventricle are muscular, and the muscles form folds and pits in the inner aspect of the wall.

The blood is discharged from the ventricle by the conus arteriosus. The conus is provided with a row of semilunar valves at each end, and it is partially divided into two longitudinal halves by a stout fold depending from the dorsal wall. The longitudinal valve is disposed in a slightly spiral direction from the right anterior aspect to near the left of

the median line posteriorly. The entrance to the pulmo-cutaneous arteries is just in front of the anterior semilunar valves and to the left of the longitudinal valve. Beyond the conus a short ventral aorta branches into the systemic and carotid arteries.

The short ventral aorta, or bulbus aortae, carries the three arches forward, dividing into right and left branches. Each

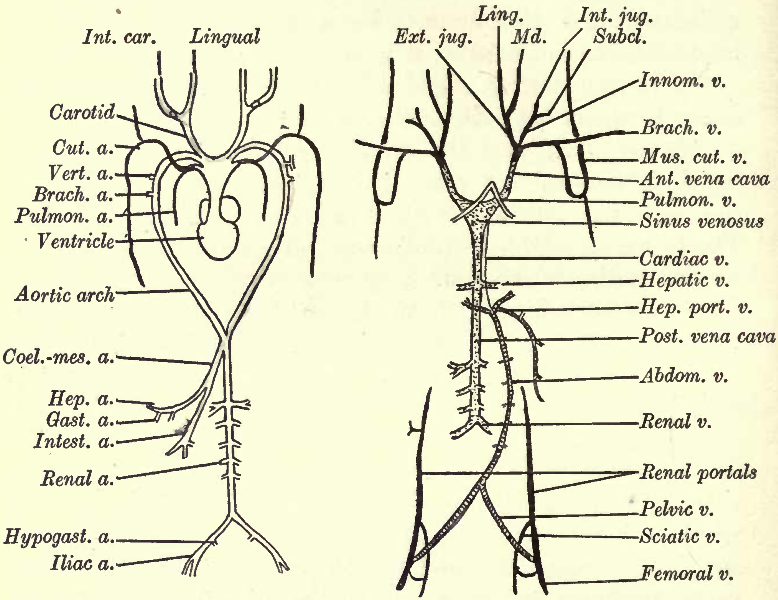


FIG. 106.—Diagrams of arterial and venous systems from the ventral aspect.

branch is made up of the pulmo-cutaneous, systemic, and carotid arteries, and these part company at about the same level. The pulmo-cutaneous divides into the pulmonary artery, which is directed to the outer aspect of the lung, and the cutaneous artery, which is distributed over a wide area of the skin of the back and head.

The two systemic vessels form an arch around the oesophagus and unite to form the dorsal aorta. The aortic arch supplies the larynx and oesophagus, and each gives off a vertebral artery to the muscles of the body wall and to the spinal

cord. On each side also a large branch arises, the subclavian or brachial artery, for the supply of the fore-limb. Just after the fusion of the two vessels of the arch the dorsal aorta passes into the median coeliaco-mesenteric artery, which descends in the mesentery to the stomach, liver, pancreas, spleen, and intestine. The dorsal aorta then passes between the two kidneys, liberating renal branches, gonadial arteries and lumbar arteries, the last to the muscles of the body wall. It terminates by dividing into the two iliac arteries which supply the hinder limbs. The iliac gives off a hypogastric

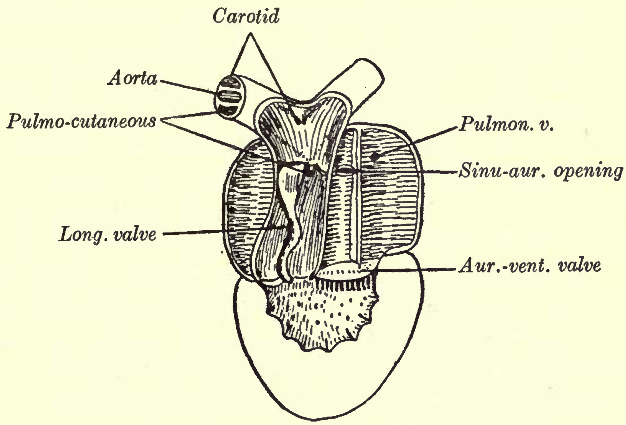


Fig. 107.—Diagram of heart. After Howes.

branch to the bladder and body wall, and afterwards divides into femoral and sciatic arteries.

The carotid divides into lingual and carotid branches. At the base of the latter is the pigmented, spongy, plexiform swelling of the vessel, the carotid gland, which interrupts to some extent the flow of blood past the point, and is probably endocrinal in function as well.

The action of the heart is a wave-like succession of pulsations beginning in the sinus venosus and ending in the conus. The valves in succession prevent the return of the blood, and thus each chamber is emptied in turn and is ready for a further supply. After the pulsation of the conus the chamber is empty, and the blood is held by the semilunar valves at the

base of the ventral aorta. When the auricles contract, therefore, and the venous and arterial blood enter the ventricle, the latter immediately contracts and the spongy walls prevent mixing, at all events on the right and left sides. The blood of the right side of the ventricle is venous, that of the left side is arterial, and the intervening blood is more or less mixed. In the relaxed condition the longitudinal valve of the conus lies over towards the right side. As soon, therefore, as the blood rushes into the ventricle from the auricles the venous blood is directed into the conus, and the pulsation of the ventricle completely fills the left side of the conus. The valve guarding the pulmo-cutaneous is overcome, and the blood enters that vessel. The contraction of the ventricle is immediately succeeded by that of the conus, and this impels the longitudinal valve to the left, thus shutting off the pulmo-cutaneous, and the more mixed blood, followed by the arterial blood, forces open the semilunar valve and gains the ventral aorta. In the ventral aorta the passage into the systemic vessels is the wider, and the mixed blood enters on each side until the pressure of the carotid, aided by the carotid gland, is overcome. The arterial blood is thus received by the vessels supplying the head.

The blood in all the different regions of the body is spread into smaller and smaller arteries and into capillaries. These reunite to form veins. The principal veins may now be referred to.

The pulmonary veins run along the inner aspect of the lungs and join above the heart to enter the left auricle by a single opening.

The blood from the head and anterior part of the body is returned to a pair of anterior caval vessels by three main vessels on each side: (1) the lingual and the mandibular join to form the external jugular; (2) the internal jugular and the subscapular form the innominate; (3) the brachial and the musculo-cutaneous join to form the subclavian. These three vessels run together to form the anterior vena cava on each side.

The posterior vena cava originates in the renal veins, receives veins from the reproductive organs, passes through

the liver, where it obtains the hepatic veins, and runs forwards to enter the sinus venosus.

There are, in addition, two important portal systems. The blood coming from each of the hinder limbs by the femoral and sciatic veins is poured by these into a single vessel at the posterior end of the body cavity. This is the renal portal vein, and it is directed forwards on the outer margin of the kidney. In the kidney the blood from the renal portal is passed into superficial venous spaces, which are supplied also by the blood derived from the renal arteries, and the mixed blood leaves the kidney by the renal veins.

The femoral vein, before fusing with the sciatic to form the renal portal, gives off a pelvic vein. The two pelvic veins unite to form the abdominal vein which runs along the body wall. The abdominal vein receives blood from the bladder by the vesical vein and from the body wall throughout its length. The abdominal vein quits the body wall opposite the liver, and after receiving the cardiac vein from the conus arteriosus it splits into two vessels which enter the two lobes of the liver.

At the point of bifurcation the abdominal vein receives the hepatic portal vein, a vessel which brings blood from the stomach, intestine, and spleen, and which before joining the abdominal vein sends a branch to the left lobe of the liver.

The liver thus obtains blood from the legs, the bladder, the body wall, and the alimentary canal, and this blood, together with that derived from the hepatic artery, is mixed in the capillaries of the liver and reaches the hepatic veins, and so the posterior vena cava.

In addition to the blood system the frog possesses a lymph system which reaches a high degree of development. It is later in appearance than the blood-vessels, and originates in spaces in the mesenchyme from the exudation of the plasma and leucocytes from the vessels, an exudation which brings oxygen and food into immediate relationship with the cells. Between the skin and body wall and the muscles of the limbs wide spaces, known as subcutaneous lymph sacs, are formed, and similar spaces occur between the peritoneum and the body wall dorsally. These and smaller spaces elsewhere

communicate with delicate lymph-vessels which amalgamate to form more distinct lymph-vessels. The lymph is restored to the blood at four points, where lymph heart dilatations are formed to pump the lymph into the blood. The anterior pair communicate with the subscapular vein at a point just behind the transverse process of the third vertebra. The posterior pair open into the femoral vein, and the heart in this case may be observed beating in the living frog on each side of the posterior end of the urostyle.

Endocrine Organs.—The spleen is derived from splanchnic mesenchyme, and is a red globular body which lies between the stomach and the large intestines. The thymus is a whitish round body which is situated just behind and above the angle of the lower jaw. It arises from epithelial buds of the dorsal region of the gills, especially from the second gill. The thyroid is double, and the two rounded masses lie on each side near the posterior cornua of the hyoid and in front of the glottis. They originate as a single outgrowth of the floor of the mouth. After it loses its connexion with the floor of the mouth it is resolved into right and left halves. The pituitary originates early in the tadpole as a median ingrowth of the ectoderm below the forebrain. A rod of cells is gradually formed which penetrates between the enteron and the brain and expands into a body behind the infundibulum. As the stomodeum is forming below, the pituitary loses its connexion with the ectoderm and, becoming hollow, is attached to the infundibulum. The adrenals have a double origin as in Elasmobranchs. The peritoneal derivative appears as paired segmental buds, practically coextensive with the pronephros and mesonephros. Sympathetic ganglia furnish the chromophile elements. In the adult frog the adrenals are elongated yellow bodies which extend along the ventral face of the kidneys. The endocrine organs have not greatly modified their functions in the land Craniates. The thymus is the organ of adolescence, and its activity, communicated by its secretion to the blood, postpones maturity. The thyroid, on the other hand, hastens maturity. Both are thus to some extent opposite, and even contending. They are related to the general well-being, and their action may influence growth. The gonads communicate their coming

maturity, impelling migration, and producing even somatic and physiological modification, as in the copulatory pad and the copulatory reflex action.

Nervous System.—The medullary canal formed by the folding of the ridges which define the medullary groove anteriorly, and the extension of the canal posteriorly after the cavity has been shut off by the development of the neurenteric canal, is resolved into an anterior brain and a spinal cord. The conversion of these into the adult structures takes place essentially as in the Elasmobranch, the difference arising by degree of development.

The brain presents clearly defined cerebral hemispheres, or prosencephalon. Behind the prosencephalon are the thalamencephalon, the optic lobes, the small transverse cerebellum, and the medulla oblongata, which narrows posteriorly to become continuous with the spinal cord.

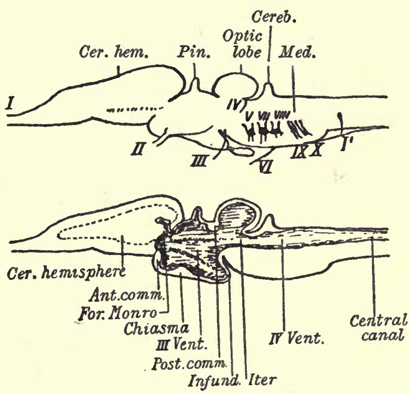


FIG. 108.—Lateral view and longitudinal section of brain.

The cerebral hemispheres are well developed. They arise as paired outgrowths of the forebrain. Anteriorly the hemispheres end in olfactory lobes which are fused. These represent the middle of the area of the forebrain, which is outgrown to form the hemisphere on each side. The rest of the hemisphere remains separate, and, fully expanded from the forebrain, it presents already areas which may be compared with those of the hemispheres of the higher Craniata. The dome-like roof, or pallial region, is separated by a slight horizontal groove, both medially and externally, from the basal region. Internally the lateral ventricles, which end blindly in the olfactory lobes and communicate with one another and with the third ventricle posteriorly, present also horizontal grooves which serve to define the upper from the basal part of the

thickened walls. All these four regions receive olfactory fibres from the olfactory lobe, and all are continued into the thalamus. The regions therefore externally may be regarded as being the primordia of the pyriform lobe above and of the corpus striatum below; and those of the inner wall, of the hippocampus above and of the paraterminal body below. The striatum is continuous with the lower part of the thalamus or hypothalamus, and the hippocampus with the epithalamus. The other two areas are continued likewise into the upper and lower moieties of the middle part of the thalamus.

As has already been made plain, the changes which take place in the conversion of the forebrain into adult structures are of a remarkable and important nature. Paired outgrowths give rise to the hemispheres and to the retina of the eye. The roof is protruded to form the pineal outgrowth and is continued into the lamina terminalis, which is continuous again with the floor. The floor presents the chiasma swelling, and is produced into a pouch-like backwardly directed diverticulum, the infundibulum, which becomes attached to the pituitary body. The side walls are thickened to form the thalamus on each side, and are put into communication by the transverse anterior and posterior commissures.

The optic lobes are prominent rounded outgrowths of the midbrain or mesencephalon, and they contain a cavity communicating with the iter. The iter expands into the large IVth ventricle, which in turn runs into the central canal of the spinal cord. The triangular-shaped roof of the IVth ventricle is bounded in front by the small, transverse cerebellum, and is otherwise a thin covering indented by a plexus of blood-vessels.

The spinal cord extends from the foramen magnum to the urostyle, where it is narrowed to form the filum terminale. It is enlarged slightly in the regions of the brachial and lumbar plexuses. It is flattened dorsoventrally, and possesses dorsal and ventral fissures.

Both the brain and spinal cord are invested by a thin pigmented connective-tissue layer, the pia mater, which conveys blood-vessels, and these expand into choroid plexuses by indenting the thin roofs of the IIIrd and IVth ventricles. The dura mater is a similar membrane investing the skull.

Between the two layers a space occurs which is lined by the arachnoid membrane formed of flattened cells, and the space is occupied by the arachnoid fluid.

The cranial nerves are developed as in the Elasmobranch, from the neural crest and the medullary tube. There are ten pairs of cranial nerves.

The nervus terminalis is represented by a slight nerve in the frog.[1] It was discovered by Judson Herrick and found by Snessarew to end in the anterior commissure, where the fibres of the pair of nerves cross, thus in the original anterior end of the forebrain.

I. The olfactory nerve arises in the olfactory lobe, and, on reaching the nasal cavity through an opening in the ethmoid cartilage, divides into two branches which spread into a large number of fibres supplying the mucous membrane of the nose.

II. The optic nerve passes from the optic lobes, forming the optic tract, meets and decussates with its neighbour in the floor of the IIIrd ventricle, forming the chiasma, and then each nerve extends freely outwards as the optic nerve. The optic nerve leaves the skull by the optic foramen and, entering the eye, expands into the nervous layer of the retina.

III. The oculomotor is a motor nerve. It arises in the floor of the mesencephalon, leaves the skull by the oculomotor foramen, which lies behind the optic foramen, and divides into branches supplying the superior, inferior, and internal recti and the inferior oblique muscles of the eyeball.

IV. The trochlear is a motor nerve. It leaves the brain, after decussating with its neighbour, just behind the optic lobes, pierces the skull by the trochlear foramen, which is situated just above and behind the optic foramen, and supplies the superior oblique muscle of the eye.

V. The trigeminal passes from the anterior end of the medulla, expands at once into the large Gasserian ganglion, and, leaving the skull by the prootic foramen, divides into two branches, the ophthalmic and the maxillo-mandibular. The ophthalmic passes above the eye structures to supply the skin of the anterior part of the head, and is sensory. The

[1] 1909, Herrick, *Jour. of Comp. Neurol. and Psych.* vol. 19; 1910, Snessarew, *Anat. Anzeiger*, Bd. 37.

maxillo-mandibular divides into the maxillary and mandibular. The maxillary supplies the lower eyelid and the skin of the side of the head and upper jaw ; it is sensory. The mandibular supplies the skin and the muscles of the lower jaw, and contains, therefore, sensory and motor fibres.

VI. The abducent arises from the floor of the medulla, and leaves the skull by the prootic foramen to supply the external rectus muscle and also the retractor bulbi muscle of the eye.

VII. The facial lies at its origin close to the trigeminal on the side of the medulla, and its ganglion, moreover, is fused with that of the VIIIth nerve. It passes from the skull by the prootic foramen. It divides into two branches: the

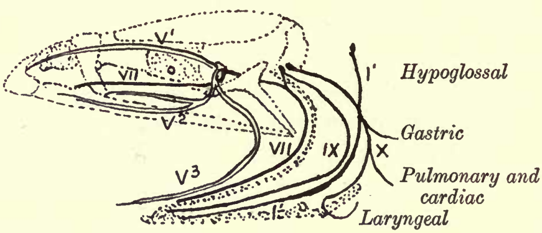


Fig. 109.—Cranial nerves.

palatine, directed to the mucous membrane of the roof of the mouth ; and the hyomandibular, which is connected to the IXth, runs along the posterior wall of the middle ear and Eustachian tube, and divides into the mandibular branch, supplying the floor of the mouth, and the hyoid branch, which goes to the muscles of the hyoid. It is a mixed nerve.

VIII. The auditory nerve enters the auditory capsule and is the nerve of the internal ear.

IX. The glossopharyngeal is the nerve of the first branchial cleft of the tadpole. In the adult it gives off a branch which crosses the columella to join the hyomandibular branch of the VIIth, and then passes on to supply the muscles and mucous membrane of the floor of the mouth. It is a mixed nerve.

X. The vagus, or pneumogastric, arises on the side of the medulla in company with the IXth, and both nerves pass from the skull by a common foramen in the exoccipital. In the larva it is the nerve of the posterior branchial clefts and the

lateralis system. In the adult it carries accessory fibres to the muscles behind the head, and, running round the oesophagus, divides into the laryngeal to the larynx, cardiac to the heart, pulmonary to the lung, and the gastric to the stomach.

The spinal nerves also number ten pairs. They are: I. hypoglossal, distributed to the muscles of the back and shoulder, and running along the floor of the mouth supplies the muscles of the floor of the mouth and tongue; II and III form the brachial plexus which supplies the muscles, skin, etc., of the fore-limb; IV, V, and VI supply the muscles and skin of the body wall; VII to X supply the nerves to the hinder part of the body and the hind-limbs, and form the lumbar plexus.

The sympathetic nervous system is plainly seen as a pigmented series of ten ganglia connected by longitudinal strands on each side of the dorsal aorta and in front thereof. Each ganglion is connected with the corresponding spinal nerve by a ramus communicans. The longitudinal nerve is continued anteriorly to the ganglia of the cranial nerves X, IX, and V.

Sense Organs.—The nasal cavity is resolved into a superior and an inferior chamber, the one opening on the surface of the head, and the other on the roof of the mouth. There is besides a lateral chamber which opens at the junction between the two cavities, and near it is the nasal opening of the lachrymal duct. The nasal membrane is formed of long columnar cells and sensory olfactory cells terminating in stiff processes.

The nose originates as a thickening of the ectoderm on each side, which becomes hollow and afterwards cup-shaped. During the larval period a solid outgrowth of cells takes place which extends to the endoderm of the roof of the mouth and, becoming hollow, establishes the posterior naris. The lachrymal duct arises also as a rod of cells from the ectoderm intervening between the eye and the nasal cavity.

The eye is covered by the conjunctiva, a transparent membrane continuous with the ectoderm of the eyelids. The sclerotic coat of connective tissue is chondrified internally and it forms the eyeball. It is pierced by the optic nerve medially, and externally is transparent, forming the cornea. The

deeply pigmented choroid coat lines the sclerotic, and opposite the rim of the cornea it is produced as the iris, the margin of which defines the pupil, and into ciliary processes. The choroid, like the sclerotic, is pierced by the optic nerve. The transparent lens is large and almost globular. It is enclosed in a thin, transparent capsule. The retina is a delicate cup-shaped membrane internal to the choroid, and ends in a rim about the level of the ciliary processes. It is made up internally of the nervous layer, and externally, next the pigment layer, of rods and cones. Between the lens and cornea the cavity is occupied by aqueous humour, and between the lens and the retina the cavity is filled with the transparent, jelly-like vitreous humour. The eyeball is moved within the orbit by the usual four recti and two oblique muscles. The optic nerve is surrounded by the fibres of the retractor bulbi which arise from the parasphenoid. Another set of muscle fibres, the levator bulbi, runs from the top of the skull under the eye to the maxilla, and the contraction of these fibres raises the eye into the projecting, prominent position. The conjunctival space gives an opening to a gland, the Harderian gland, the products of which are conveyed into the nose by the lachrymal duct. The eye originates in the manner already described in the previous chapter. The lens is almost fish-like in character. The eye is well developed and is designed to focus the rays of light coming from the field of vision on that occupied by the rods and cones of the retina. The rays pass through the transparent elements mentioned, and the focus is adapted to distance by changing the shape of the lens. This is accomplished by relaxing or compressing the capsule of the lens by means of the muscles of the ciliary processes which lie all round the lens and to which the capsule is attached. The quantity of light entering the eye is regulated by the dilatation or constriction of the iris. Moreover, the eye is brought into position by the contraction of the levator bulbi muscle and rotated as required by the other muscles.

The internal auditory labyrinth is like that of the skate, and it has a similar development from the ectoderm. It consists of three semicircular canals, each expanded into an ampulla. The canals open into a common sac, the utriculus,

and this opens widely into the sacculus, which bears a lobe, the lagena, identified with the cochlea of higher vertebrates. The utriculus opens into a small ductus endolymphaticus. The whole labyrinth is distended by endolymph and lies in the auditory capsule, which, as has been noted, is formed of cartilage and of bone. The narrow space between the internal ear and the capsule is occupied likewise by a fluid, the perilymph. The auditory nerve splits into branches on entering the capsule of the ear, and these end in special sensory areas—in the ampullae, utriculus, and sacculus. The endolymph provides calcareous granules which are related to the sensory cells in these regions. An important modification is related to the ear externally to the capsule. The Eustachian tube

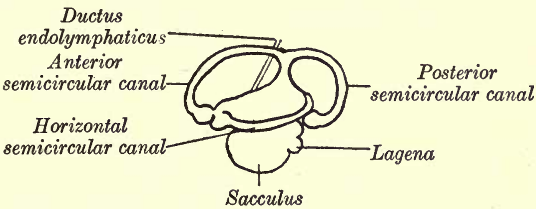


Fig. 110.—Auditory organ.

represents the spiracular cleft of the fish, and it expands as a cavity which penetrates in the space above the quadrate and forms the cavity of the middle ear. The cavity comes into close relationship with the skin and forms the tympanum or drum, and to this, as has been explained, the columella auris is applied ; the other end of the columella ends in the stapes. The sound waves of the air, therefore, cause the thin tympanum to vibrate, and the vibrations are communicated to the stapes and so to the fenestra ovalis. They thus reach the perilymph and, through the thin wall of the labyrinth, the endolymph ; and the waves, now fluid waves, set the otoliths or calcareous granules in motion and the sensory cells are affected. The endolymph also, by its movements in the semicircular canals, is constantly communicating to the brain changes in position and direction and in equilibrium.

Urinogenital Organs.—The pronephros functions as the kidney in the larva. It arises in the nephrotome mesoderm

just below the body myotomes 3 to 5. A thickening appears on the outer wall about the period of hatching, and it is converted into a longitudinal groove which differentiates into an outer pronephric duct and three tubules which open into the body cavity, each of the three openings being a nephrostome. The pronephric duct grows posteriorly and establishes a communication with the cloaca. The three tubules and the duct joining them become convoluted and they are surrounded by the posterior cardinal vein. The aorta also, opposite the pronephros, sends out a short pronephric artery which breaks up into a glomerulus distending the peritoneum underneath the nephrostomes, thus independently of the tubules. It would appear, therefore, that water derived from the glomerulus and coelomic fluid is drawn in by the nephrostomes, and the excretory products are removed by the tubules from the blood of the cardinal vein.

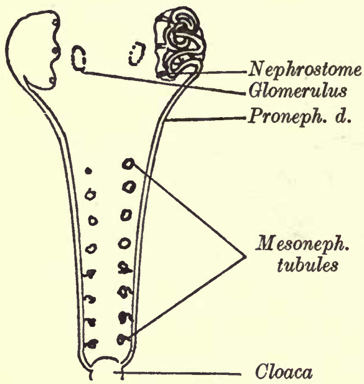


FIG. 111.—Pronephros and developing mesonephros of tadpole.

The mesonephros appears about the end of the larval period. Segmental masses of mesoderm left after the separation of the myocoels from the splanchnocoel posteriorly to the pronephros, in the region therefore previously occupied by the nephrotomes, become hollow and form tubules. The tubules are put into communication with the pronephric duct. Each tubule grows and becomes convoluted, and on its medial side forms a Malpighian body consisting of a Bowman's capsule and an arterial glomerulus, and the tubule extends to form a nephrostomal communication with the splanchnocoel. As the mesonephros increases in size by growth of its tubules and the establishment of accessory tubules, the pronephros degenerates. The degeneration is followed by the atrophy of the anterior tubules of the mesonephros. The remaining

mesonephric tubules lose their communications with the splanchnocoel. The nephrostomal part of the tubule in each case is cut off from the Malpighian body, which thus becomes terminal, and it establishes an opening into a factor of the renal veins.

The gonads appear as ridge-like thickenings of the peritoneum medial to the mesonephros. In the male the ducts of the testis on each side are connected with the anterior Malpighian bodies into which they open. The mesonephric duct of the male thus is also a gonoduct. The kidney is the Wolffian body, and its duct the Wolffian duct. In the females the ovaries are not so connected, and the mesonephric duct

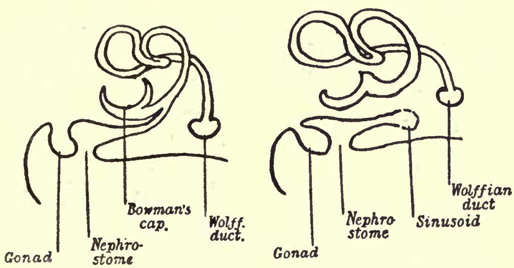


Fig. 112.—Transverse sections illustrating two stages in the development of the mesonephric tubule.

functions only as a ureter. The oviduct, or Müllerian duct, is like that of the Elasmobranch, and it opens anteriorly into the body cavity. It has been said to be developed by a splitting of the pronephric duct as in the Elasmobranch, but most observers state it is developed independently from a groove which forms in the peritoneum. The bladder is developed as a ventral outgrowth of the cloaca.

In the adult frog the kidneys lie one on each side of the vertebral column in the abdominal lymph space. They are elongated red bodies and are traversed ventrally by the yellowish adrenal. The tubes of the kidney filter water from the blood at their commencement in Bowman's capsules. The arteries entering the kidney give rise to a multitude of glomeruli, and the efferent vessels run into sinusoids, where they are joined by the branches of the renal portal. Both these, therefore, contribute to the capillaries which surround

the tubules, and the blood is gathered and discharged by the renal veins. The tubules of the kidney all open into the mesonephric duct, which is the ureter. It runs down the outer edge of the kidney and, reaching the cloaca, opens separately from its neighbour on the dorsal wall. The anterior end of the genital ridge, in degenerating, forms the rudiment of the fat body, which undergoes expansion in the adult as conspicuous lobed yellow bodies placed in front of the kidneys.

In the male the testes are oval yellow bodies. The sperms liberated from the walls of the tubules are conveyed from the

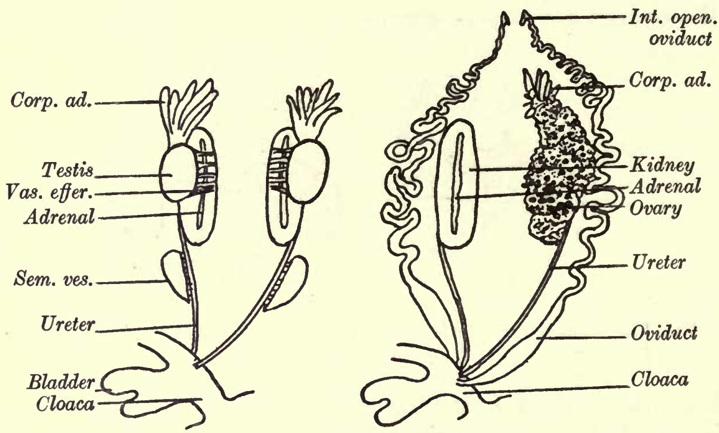


FIG. 113.—Male (left) and female (right) reproductive organs.

testes by a series of vasa efferentia on the inner anterior aspect of the kidney. They are conveyed into the mesonephric duct, which, in addition to acting as a ureter, is a vas deferens. In the male, moreover, the vas deferens is produced by a series of small ducts into a triangular-shaped body on its lateral surface. This is the seminal vesicle.

In the female the ovaries are large irregular masses containing eggs at all stages of development. At the breeding season many of the eggs become ripe, and are shed into the peritoneal cavity. They are conveyed forwards to the small opening of the oviduct. The two openings lie close together on each side of the oesophagus, and lead into the long

convoluted oviduct or Müllerian duct. The darkly pigmented eggs are coated with a thin layer of albumen by the glandular secretion of the oviduct. At the lower part of its course the oviduct widens, forming a cavity in which the eggs may remain before being deposited in the water.

During the breeding season, in early spring, the male grasps the female, the anterior limbs with their swollen pads being firmly flexed around the pectoral region of the female. The eggs and the sperms are discharged simultaneously, and fertilisation takes place in the water.

Development.—The eggs shortly after extrusion become distended by the absorption of water in the albumen layer, and the whole of the eggs laid form a floating mass at the surface. Each egg is surrounded by a vitelline membrane around which the albumen layer forms a thick coat of a protective nature. The egg is darkly pigmented, and the warmth obtained from the rays of the sun is retained in contact with the albumen, better at least than it would be in contact with water.

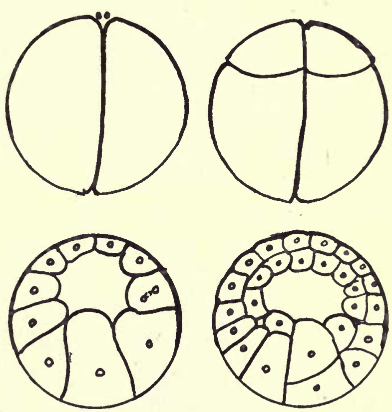


FIG. 114.—Segmentation of egg and beginning of delamination. After Marshall.

The first polar body is liberated when the egg becomes ripe in the ovary, and the second, when the egg is extruded and when the sperm gains entrance, as a preliminary to fertilisation.

Segmentation is holoblastic, and the first two furrows are mutually at right angles through the polar field. The egg is thus orientated as in Amphioxus. The third cleavage is at right angles to both the others, and separates the more animal from the more vegetable region. Thereafter the cells at the animal pole divide the more rapidly, and a blastula is formed consisting of small pigmented cells at the animal pole and of larger and fewer white cells at the opposite pole, and enclosing

a segmentation cavity. The condition is almost exactly that of Amphioxus; but invagination is impossible, and the cavity is narrowed by the delamination of cells into the interior. Most are formed by the endoderm, but, as Samasso's experiment indicated, they arise also from the margin of the ectoderm and endoderm. The segmentation cavity is thereby converted into an enteron. The subsequent events show, however, that the delamination resorted to is not strictly comparable to that of the Coelenterates, but is a process brought about by the increase in yolk of the endoderm cells at the vegetable pole preventing invagination. A blastopore is formed at the margin of the ectoderm and the endoderm—that is, about midway between the two poles of the egg. And it is widely distended by the yolk cells of the endoderm. It will be observed that the condition is similar to that of the Elasmobranch, but the yolk is so massive in the egg of the Elasmobranch as to bring the blastopore close to the animal pole.

The margin of the blastopore advances over the yolk cells, the process beginning at the dorsal lip and extending to the ventral. The blastoporal rim gradually narrows, therefore, as it approaches the vegetable pole, which is the posterior pole. This pole of the egg is white, and the yolk cells stand out in relief as the darkly pigmented ectoderm advances over them. The narrowing white area is called the yolk plug. It is reduced to a white spot, and is finally obliterated with the formation of the neurenteric canal. Gastrulation may be said to be ended, therefore, as soon as delamination has taken place and the margin of the blastopore has appeared. The subsequent changes relate to the postgastrula.

The backward growth of the dorsal lip gives rise to an extension of ectoderm and endoderm and the formation of mesoderm. An enteron is thus formed immediately underneath the dorsal lip, and it is extended by the growth of this region of the blastopore. But it also excavates its way among the delaminated endoderm. The endoderm at the same time gradually encloses the primitive enteron. When the blastopore approaches the posterior end of the egg the enteron undergoes a large expansion, one cavity resulting. The primitive enteron is said by some observers to disappear in the

endoderm at the anterior end, but it usually, if not always, takes its place by the excavation of the intervening cells as the front end of the enteron (fig. 115).

The blastopore, as it narrows and closes at the posterior end of the embryo, forms a vertical slit, a short primitive streak and groove.

As these changes are approaching completion the dorsal ectoderm is thickened and flattened. This is the neural plate,

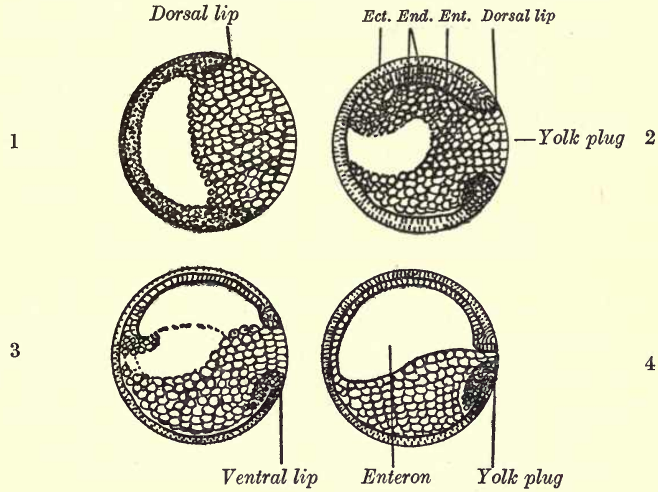


FIG. 115.—Longitudinal sections of postgastrula stages to illustrate the overlapping of the delaminated endoderm by the blastopore. The primitive enteron, often called the segmentation cavity, is united to the secondary or neurenteric enteron by an absorption of the cells intervening between them. These figures are rotated about 90° compared with those of fig. 114.

and it becomes further defined by the appearance of the neural fold, which arises anteriorly, and transversely, to mark the anterior limits of the plate and extends backwards on each side until it reaches the middle of the primitive streak, thus defining a neurenteric groove. It is further defined by the appearance of a median groove which begins at the dorsal lip of the blastopore and extends forwards in the mid-line of the neural plate. The neurenteric groove is converted into the neurenteric canal by the fusion of the neural folds, and the fusion is continued forwards, with the result that the neural

plate is converted into the neural canal. The shutting in of the neural canal and the neurenteric canal is followed by a closing of the lower part of the blastopore, but this lower part of the blastopore persists as a pit which marks the later formation of the anal opening. The blastopore is thus converted above into the neurenteric canal and below into the anus.

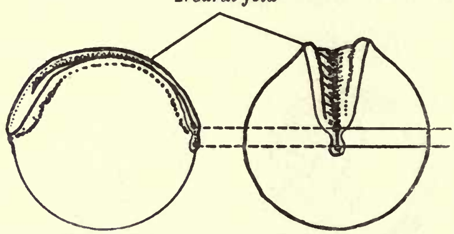


FIG. 116.—External views of embryos to show the early condition of the neural plate and the fate of the blastopore.

After the closing of the neurenteric canal the neural canal is extended as a tube. The anterior end of the tube is wide, is bent downwards, and already presents the features of the forebrain. The midbrain occupies the angle of bending, and the hindbrain is horizontal and passes into the spinal cord.

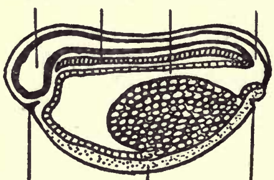


FIG. 117.—Diagrammatic longitudinal section of embryo. After Marshall.

The endoderm, after the formation of the neurenteric canal and the closing of the blastopore, encloses the enteron as a cavity which is closed but communicates with the neural canal posteriorly. It consists of a single layer dorsally and laterally, but below its floor and sides are occupied by the many-layered yolk cells. The growth which proceeds at the posterior end forms the tail and extends the cavity beyond the point which marks the position of the anus, and this extension is called the postanal enteron and endoderm. The

cavity is put into communication with the exterior by the enteron posteriorly establishing an opening with the small proctodeum provided by the remnant of the lower lip of the blastopore, and this is speedily converted into the cloaca by the entrance of the pronephric ducts.

At this stage, therefore, the embryonic enteron is resolved into a wide pharyngeal cavity anteriorly, at the posterior end of which the liver is indicated as a small diverticulum, and a flattened cavity which communicates with the exterior by the cloaca and extends onwards as the postanal enteron to the neurenteric canal. The gills are formed in the pharyngeal region by outgrowths of the endoderm meeting small invaginations of the ectoderm, and the mouth by a shallow ingrowth of the ectoderm, the stomodeum, which meets and fuses with the anterior wall of the enteron.

The notochord is formed from the dorsal endoderm. During the early growth of the dorsal lip two layers only concern this region of the blastopore, the ectoderm above and the endoderm below. The latter is the seat of formation of the notochord. A thickening takes place by multiplication of cells, and the notochord is separated from the roof of the endoderm by simply splitting off from it, and in the process the endoderm may contribute further cellular elements below the notochord, as the so-called hypochorda. The edges of the primitive chorda are continuous with a sheet of mesoderm which is formed by the rest of the lip of the blastopore, and as the notochord separates from the endoderm so does it separate from the rest of the mesoderm. A median notochord is thus formed, and two wings of mesoderm. These are at first directly continuous, and the mesoderm of the ventral lip of the blastopore with the yolk cells of the endoderm. The separation of the notochord from the endoderm is accompanied by the appearance of a pair of grooves, one on each side of the notochord, which indicates a contribution of cells from the endoderm in the formation of the myotomes, and is further interesting in relation to the formation of the myotomes in Amphioxus and in the fish. The mesoderm thus reinforced forms a sheet extending from the notochord, and it gradually meets and fuses underneath the endoderm. This sheet of mesoderm on each side

is resolved into the paired myotomes above and the splanchnic mesoderm below. Both ultimately develop cavities, forming the segmented myocoels and the splanchnocoel. Head and mandibular cavities are not formed as such, and the eye muscles appear to be developed from solid groups of mesenchyme.

When the larva escapes from the egg it is in an incomplete state of development. The mouth and the gills can be seen as grooves externally, but they are not perforated; the cloaca is the only opening. Behind the region of the mouth

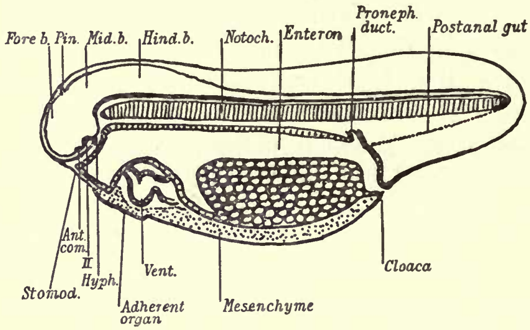


Fig. 118.—Diagrammatic longitudinal section of tadpole at hatching. After Marshall.

a horseshoe-shaped pit is formed which is glandular and acts as an adhesive organ or cement gland. With this the larva attaches itself to the albuminous mass from which it has escaped, and afterwards to plants. The cement gland prevents the larva falling into the mud at the bottom of the pond. The ridges between the gill grooves develop tuberances, at first two pairs and then three pairs, which grow out into branching, vascular, external gills. Many of the ectodermal cells of the body are ciliated. The larva continues to grow, using up the yolk contained in the cells of the floor of the enteron. The tail gains in length as a laterally flattened structure, provided above and below with median membranous fins and containing an extension of the notochord and myotomes, which, as in fishes, are <-shaped. As it lengthens, the postanal endoderm degenerates into a rod of cells and

disappears. Such is the tadpole larva, and it serves as a fish-like stage to a creature which finally becomes a lung-breathing animal.

Of the gill clefts the first pair, or spiracles, are not put into communication with the exterior, but this internal pouch of the endoderm is converted into the Eustachian tube and the middle ear. Four clefts are perforated behind this one. With these clefts are associated the hyoid and four branchial arches. The hyoid arch is developed behind the spiracle, and the branchial arches behind the corresponding branchial clefts. The external gills are produced from the first and second branchial arches, and these are followed later by a smaller outgrowth of the third arch and small protrusions of the fourth arch. These function at the early period of larval life. In about three days after hatching the mouth and the branchial clefts are perforated. The latter develop internal gills in the form of tufts of the walls of the margins of the clefts. Respiration is now carried on by the water being brought into the pharynx through the mouth and passed over the internal gills. Just before this happens the wall of the hyoid region grows out as a backwardly directed fold on each side to form the operculum, or gill cover, and the water escaping from the gills passes out at a single opening. This is different from the conditions in the skate and its allies, but it is exactly parallel to what happens in the majority of fishes. The extension of the operculum is accompanied by a degeneration of the external gills, and the gill opening of the right side is closed completely during a period when the left gill opening remains patent and functional, discharging both gill chambers.

The mouth of the tadpole is furnished with horny jaws, upper and lower, supported by the cartilages of the jaws, and at the sides the mouth is produced into horny papillae. The horny apparatus is derived from a cornification of the ectoderm, and it is lost by a shedding of this layer at metamorphosis. As the tadpole increases in size and gains in strength the adhesive organ degenerates. It becomes split into two, decreases, and finally disappears. Cutaneous sense organs are developed in rows on the larva, forming a lateralis system which is lost at metamorphosis.

The heart of the tadpole in the early stages is fish-like. It consists in succession of a sinus venosus, an auricle, a ventricle, and a conus arteriosus. The latter is put into communication with the external gills by four afferent branchial vessels which develop from a common trunk in regular succession, the first being the first formed. The blood is led in efferent branchials to the two dorsal aortae. The aortae send the blood into the head by carotid arteries, and, uniting behind the gills, carry the blood to the posterior end of the larva.

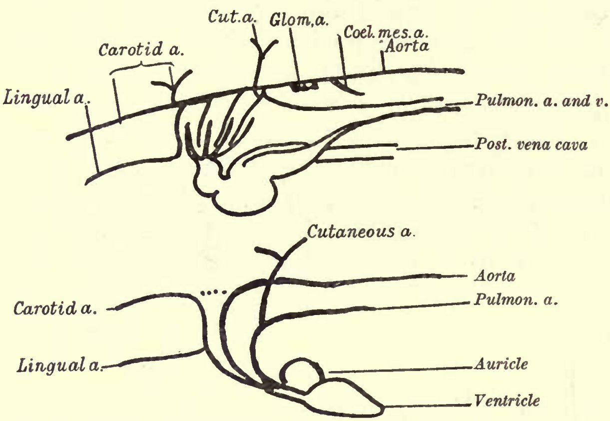


FIG. 119.—Lateral diagrammatic views of arterial circulation of tadpole and frog.

The venous blood is carried back to the heart by a sub-intestinal vein, and by cardinal veins which form a Cuvierian vein on each side to enter the sinus venosus. The circulation, therefore, is that of a fish. With the appearance of the internal gills the blood is more and more sent to them, and the circulation to the external gills is correspondingly reduced.

The length of the tadpole stage of the life of the frog depends on circumstances, and if means be taken to prevent the tadpole gaining the surface it may be prolonged, large tadpoles resulting. In some cases, as that of Axolotl, the call to the adult state may be postponed for an indefinite number of generations, the creature reproducing in the meantime as a larva. In the case of the frog the change usually takes place after about three months.

The metamorphosis is ushered in by the appearance of the limbs and the development of lungs. The auricle becomes divided into two chambers by the appearance of a septum which springs from the dorsal wall, and at the same time the conus develops the longitudinal valve, which may be regarded as a septum which remains incomplete in the frog. A pulmonary vein is established between the smaller left auricle and the lung, and the fourth branchial arch yields a branch which goes to the lung. It also subsequently sends a branch to the skin. The fate of the four branchial arches may be simply said to be : the first forms the carotid, the second the systemic or aorta, the third disappears, and the fourth, losing its connexion with the dorsal aorta, becomes the pulmo-cutaneous. The gills cease to function, and the lungs are used, together with the skin, for respiration. The intestine of the larva is conspicuously long and folded in a spiral. Towards the end of the tadpole life it gradually loses this condition, and with the cessation of feeding at metamorphosis it actually becomes shorter. The horny jaws are discarded, and the mouth is enlarged, together with the tongue. The eyes are also expanded, and with the appearance of the hind-limbs, and then of the fore-limbs, and the atrophy of the tail, the conditions of the adult are practically reached. The tail shrivels up by a breaking down of its elements, which are carried away in the blood, the process beginning at the tip. When the metamorphosis is completed the young frog migrates from the water.

CHAPTER XI

THE DEVELOPMENT OF BIRDS AND MAMMALS

Phylum VERTEBRATA
Sub-Phylum CRANIATA
Class AVES
MAMMALIA

REPTILES, Birds, and Mammals are grouped under the name Amniota for the reason that the embryo is enclosed in an envelope, called the amnion. The early history of the chick illustrates the formation of the amnion and of other embryonic membranes. A study of the development of birds, still better that of reptiles, is a necessary preliminary to an understanding of the changes induced by the uterine period of life of mammals. The material for a study of the embryology of the chick (Gallus) is easily obtained ; but although birds are very consistent in their development, important points are better displayed in the embryology of the less modified sea birds.

The eggs of birds and reptiles, like those of the Elasmobranchs, are large and meroblastic, and in the case of some of the extinct species of birds they reached a gigantic size. The nucleus is superficial, and the cytoplasm is distended by a large provision of food material, the yolk. It is covered by a vitelline membrane, and during its passage down the oviduct it is coated with layers of albumen, the white of the egg. The egg during its descent is rotated around the oviduct, and the albumen is coiled in front and behind the yolk into spiral processes termed chalazae. In the lower part of the oviduct the outer layers are hardened to form a double shell membrane,

the two layers of which are separated by the air space at the broad end, and a limy secretion gives them a final covering of a calcareous shell which in most birds receives besides a deposition of pigment. The sperm has the usual flagellate structure, and is provided with a long head terminating in a sharp process. Fertilisation takes place in the upper part of the oviduct. As in Elasmobranchs, several sperms enter the egg, but fertilisation usually is effected by one, the rest during development being kept outside of the area of segmentation.

Blastoderm.—Segmentation takes place in the oviduct and results in the formation of a white patch of cells at the animal pole, the blastoderm, known also as the cicatricula, or tread. During the process of segmentation in the oviduct a superficial layer of cells is developed which yields by horizontal divisions cells underneath, and the blastoderm reaches a thickness of several layers. This is resolved into a layer of ectoderm in the form of a single layer of cylindrical cells, and an endoderm which is being reduced to a single layer in the middle of the blastodermal area, but still is many-layered at the margin. Between the two a segmentation cavity is indicated. It is in this condition usually that the egg is laid, and in this phase it may remain for a long period in a suspended state of development, and it does not undergo further developmental changes until it is placed in a temperature approaching that of the bird (fig. 120).

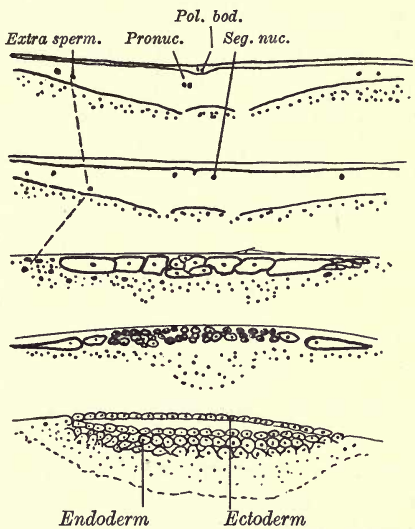


FIG. 120.—Segmentation. The upper four figures refer to the pigeon, and are after Blount; the last figure to the fowl, and is after Duval. The stages represented take place in the oviduct.

With the beginning of incubation, cell multiplication is started afresh and the blastoderm is extended all round its margin. It is now clear, as indeed is usually clear at the time of laying, that the blastoderm is resolved into a central transparent area, the area pellucida, and a marginal denser area, the area opaca. This is due to the thinning of the endodermal layer referred to above. The margin of the blastoderm makes rapid progress, and it is of interest that the two layers are separated in the process, the ectoderm advancing in front of the endoderm. In about three days the sphere of yolk has been half encompassed, and afterwards the two layers advance more leisurely over the lower hemisphere.

The blastoderm consists, as has been said, of two layers, a thin ectoderm and an endoderm which is thin below the pellucid area and is many-celled and thick all round the margin, forming the area opaca. The central pellucid area is the scene of changes which produce the embryo. Not long after incubation is started the central ectoderm of the area becomes thickened, marking the embryonic area; and at or near what proves to be the posterior end of the area pellucida, the ectoderm commences to proliferate, forming a medial ridge projecting downwards, and the ridge at once liberates mesoderm cells which migrate outwards from it between the ectoderm and the endoderm. The thickening spreads forward in the pellucid area, and wings of mesoderm are developed from it. Near the middle of the area pellucida the ectodermal ridge comes to an end, and at this point a deeper extension of the proliferation unites the two layers. In front of the place of fusion proliferation still takes place, but from the endoderm in the same longitudinal direction, and this endodermal proliferation extends forwards to a point nearly midway between the place of fusion and the anterior limits of the thickened ectoderm which defines the embryonic area. These changes occur almost simultaneously early in the first day. It is not altogether a local proliferation, but the result of growth in front of the region of fusion.

The forward endodermal thickening which takes place in a linear manner, marking the longitudinal axis of the embryo, is the notochord; and the thickening associated with the

ectoderm is the primitive streak. The streak is at once further defined by a groove which runs also longitudinally, and this is called the primitive groove. It is produced by an infolding

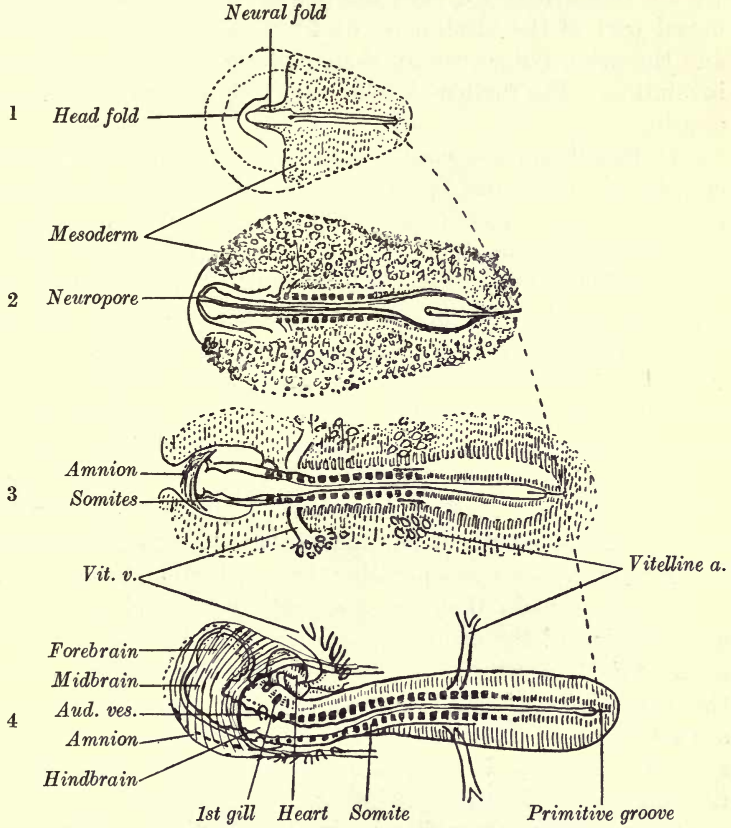


Fig. 121.—A series of four diagrams to illustrate the condition of the embryo (1) near the end of the first day of incubation, (2) beginning of second day, (3) middle of second day, and (4) end of second day. The primitive streak in each is connected by a dotted line.

of the ectoderm. At its forward end the primitive groove forms a pit, and in aquatic and some other birds this pit is still more distinctly infolded to form an opening into the mass of cells which unites the ectoderm with the endoderm. This pore is also developed in the blastoderm of reptiles, and becomes an opening into the enteron. In the case of the birds mentioned,

also, the pore may be put into communication with the enteron. The opening thus formed is at a later period converted into the neurenteric canal. From these considerations we are thus led to see that the pit, or Hensen's knot, is the dorsal part of the blastopore, its front margin the dorsal lip, and the primitive groove an elongated part of the blastoporal involution. The further development indicates this still more clearly.

At first there are simply two layers, the ectoderm and endoderm. With the appearance of the notochord and the primitive streak, mesoderm is rapidly developed as a layer intervening between these, and it is the development of the mesoderm which marks the beginning of the activities of the primitive streak. The notochord at its anterior end is formed by a proliferation of the median endoderm, and as it is becoming separated from the endoderm, by splitting off from it, a pair of endodermal grooves is formed, which give off mesoderm, also extending outwards. The mesoderm is slightly developed in front but increases posteriorly to the primitive streak, and thus a continuous mass of mesoderm is produced extending over the whole length of the notochord and primitive streak and forming two wings separating the ectoderm and endoderm.

It is thus plain that the gastrulation takes place by the delamination of the endoderm, and that the blastopore arises as an infolding which rapidly becomes longitudinal. With the appearance of the blastopore the gastrula changes into a postgastrula. The blastopore is not marginal in birds and reptiles, but is formed, as in Amphibia, as an infolding of the outer layer of cells.

The procedure thereafter is simple and direct. The ectoderm in front of the blastopore gives rise to the neural plate, and it is delimited by the appearance of neural folds. The endoderm below yields the notochord medianly, and it is at first continuous with the mesoderm, which, as has been seen, is formed besides from the lips of the blastopore—that is to say, the primitive groove.

The nervous system is developed from the ectoderm in front of the point marked by the anterior end of the notochord, thus from the gastrula, and from the ectoderm up to the dorsal

lip of the blastopore. As the area pellucida lengthens, becoming oval, pear-shaped, and then hourglass shaped, the neural plate is gradually extended and the blastopore is carried backwards. The neural folds become more distinct and, as in

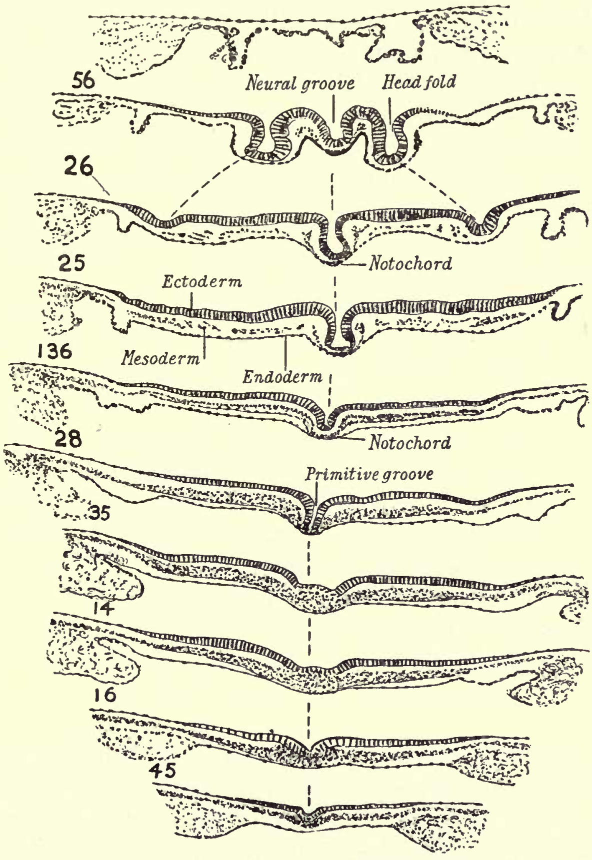


FIG. 122.—Transverse sections of a lesser black-backed gull in the stage of fig. 121 (1). The numbers refer to the number of sections of 8μ intervening between the sections drawn.

the other cases we have examined, they limit the nervous system in front transversely and extend backwards as diverging folds, ending, as in the case of the frog, on each side of the primitive groove. During the first day, as the neural area

increases in length the folds in the forward region approximate and later fuse. The fusion, however, is not terminal, a wide but narrowing neuropore being left.

The anterior end of the head is early during the first day marked by a fold, the head fold, which extends as a wing on each side of the developing brain. The groove in front of the fold deepens, and as it deepens the head is rotated forwards, carrying the brain with it. The fold occurs in the gastrula region in front of the brain, and consists merely of ectoderm and endoderm, and both these layers are concerned. The head is now marked as a process free from the underlying blastoderm, and the head process contains an anterior diverticulum of the endoderm. The process is exactly similar to that which takes place in the Elasmobranchs.

During the second day the closing in of the neural canal proceeds posteriorly, but it remains open at the posterior end, where the folds diverge and approach again on each side of the primitive streak. The brain is now plain as a wide region of the neural canal. The neuropore is closed, but the front end of the brain and the ectoderm remain connected for a time. The brain is being bent downwards, undergoing a mesencephalic flexure. It is resolved into fore-, mid-, and hind-brains, the latter passing insensibly into the spinal cord. The forebrain is expanded laterally into large optic cups, and later into paired hemispheres. Towards the end of the second day the sinus at the posterior end of the neural canal closes to form a narrow slit, and the head becomes still more flexed and is directed to the right.

During the third day the mesencephalic flexure is carried so far as to bring the anterior end of the head into a backwardly directed position, and the twisting of the head to the right side to the extent that the plane of the head is parallel to the underlying blastoderm. The torsion is continued until finally the rest of the body occupies this position.

The posterior lips of the neural folds now meet and fuse, with the result that the anterior portion of the primitive groove is enclosed in the canal and the posterior is shut out. The former is later in some birds, as has been said, converted into the neurenteric canal; and in the chick the medullary

canal and the endoderm are placed in communication by an undifferentiated mass of multiplying cells which runs round the posterior end of the notochord.

The shutting in of the neural canal posteriorly is accompanied by a folding of the embryo immediately behind: this is the tail fold; and the folding in front and behind the embryo

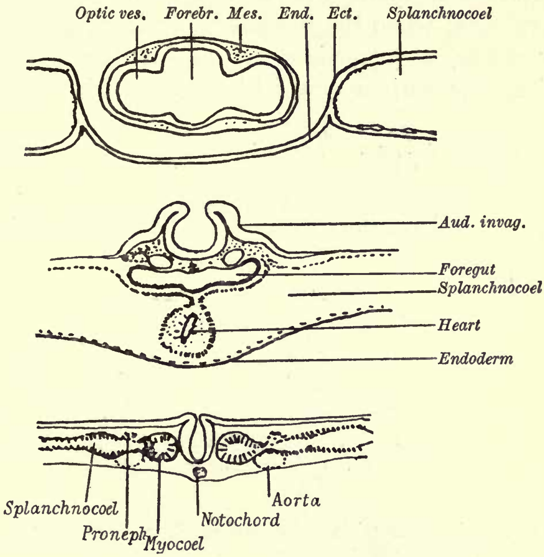


FIG. 123.—Three transverse sections of second-day fowl, the first through the optic cups, the second through the auditory invagination of the ectoderm, and the third through the body behind the head.

gradually extends, with the result that the embryo is raised and defined from the blastoderm. The growth after the formation of the tail takes place by a general expansion of the embryo, and in length by the continued growth of the tail fold—that is to say, of the region occupied by the dorsal lip of the blastopore. The ventral part of the blastopore by the formation of the tail fold is bent under the embryo, and from it later the proctodeum is developed.

While these changes have been proceeding the ectoderm and the endoderm have made immense progress in investing the yolk. The blastoderm has extended over more than half

of the yolk, and the two layers are accompanied by the intervening mesoderm. As has already been plain, the mesoderm extends outwards from the embryo on each side and posteriorly, and it has been resolved also into somatopleure and splanchnopleure. In front of the head the mesoderm is absent. The mesoderm-free region, however, is gradually narrowed by the mesoderm increasing in a fold from each side. During the second day, when the head is being formed and is being bent downwards, a depression forms below the head, and in association therewith a new fold is produced in front.

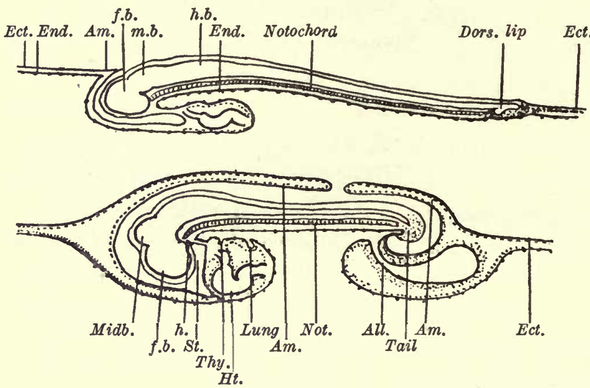


FIG. 124.—Diagrammatic longitudinal sections of second- and third-day fowls to illustrate the development of the amnion and the allantois.

f.b., m.b., h.b., = fore-, mid-, and hind-brain; *h.* = hypophysis; *St.* = Stomodeum; *Thy.* = thyroid; *Am.* = amnion; *All.* = allantois.

Amnion.—This fold is the rudiment of the amnion. It consists of ectoderm and endoderm. But as it forms, the mesoderm wing on each side invades the region, and the two layers, united at the edge, rapidly separate the endoderm from the ectoderm. This is followed by an expansion of the body cavity, which has the effect of removing the endoderm of the primitive fold to a ventral position. The ectodermal fold, together with the somatopleure mesoderm, is continued backwards as the embryo sinks into the yolk. With the formation of the tail fold a similar amnion fold appears around the hinder end of the embryo. These folds rise and fuse as they advance along the sides of the embryo. The process makes great progress in the

third day, and in the fourth the fusion of the amnion folds is completed. The result of the fusion is that an inner layer of ectoderm, continuous with that of the embryo, forms a cavity around the embryo—the amniotic cavity—while the outer layer of the fold continuous with the ectoderm of the blastoderm is cut off from the embryo. The first is called the amnion, or the true amnion, and the second the false amnion, or serosa. The amnion increases in size with the increase of the fluid which it contains, the amniotic fluid. As the embryo becomes constricted from the yolk, it is more and more surrounded by the amnion and the amniotic fluid, and development proceeds therefore in what might be called aquatic conditions.

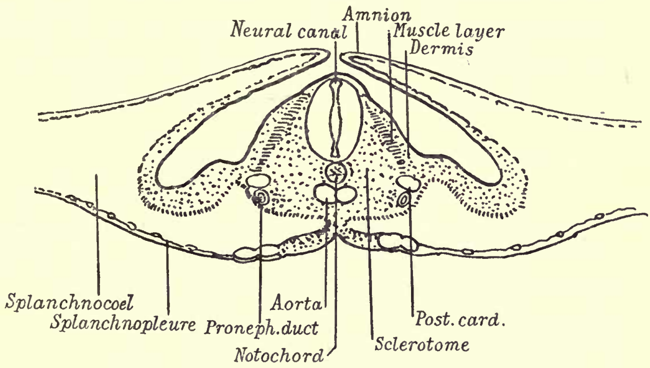


Fig. 125.—Transverse section of body of third-day fowl.

Yolk Sac.—The endoderm, to begin with, is a layer of flattened cells next the yolk, and the primitive enteron lies between the two. With the formation of the head and tail folds the enteron becomes tubular in front and behind. It may be said, therefore, to be resolved into three regions, fore-, mid-, and hind-gut, the mid-gut being that part of the endoderm which lies over the yolk and expands on each side as the endodermal part of the blastoderm. Both the fore-gut and the hind-gut, but especially the former, increase in length with the growth of the embryo, and the mid-gut becomes reduced to a small portion of the enteron. At this place, however, its floor is continued as a tube-like outgrowth which rapidly widens to form the endoderm of the yolk. The investment

of the yolk continues by the endoderm, and as the embryo increases in size the yolk thus invested appears as a sac depending by a neck of ectoderm and endoderm, each reinforced by a layer of mesoderm, the ectoderm expanding into the amnion and the endoderm investing the yolk. It is now called the yolk sac, and the neck the umbilical cord.

The **allantois** is developed as an outgrowth from the floor of the hind-gut. The allantois, carrying the mesoderm with it, grows into the splanchnocoel below the gut, invades the umbilical cord, and expands into the extra-embryonic body cavity to apply itself against the serosa. The mesoderm of the allantois unites with that of the serosa, and the allantois gradually spreads over the inner surface of the serosa—first above the embryo, but, extending downwards on all sides, it separates the serosa from the endoderm of the yolk and finally completely surrounds the serosa. It is, as we shall see, used for respiration.

Within the embryo the endoderm has in the meantime been making important advances. Its anterior end is met by an invagination of the ectoderm, which is the stomodeum, and which yields the hypophysis or pituitary body as an outgrowth which becomes attached to the infundibulum. Before the enteron and the stomodeum have been put into communication by the breaking down of the double wall which separates them, this front end of the enteron is expanded as the pharynx and is produced laterally into a series of clefts. These are the hyoid and the first, second, and third branchial clefts, and in the walls separating them visceral arches are developed. The clefts and the arches correspond exactly with those of the fish and the amphibian, but they do not form gill folds. They meet and fuse with corresponding ectodermal invaginations which form distinct external grooves along the neck region. They all disappear except the hyoid cleft, which is retained to form the Eustachian tube and middle ear.

The floor of the anterior part of the enteron is produced into a pouch which becomes the thyroid. The thymus is produced from the branchial clefts. The stomach and intestine are gradually formed from the enteron as development proceeds, and outgrowths give rise to the lungs and the glands.

At the hinder end of the embryo the hind-gut comes into close relationship with the ectoderm at the posterior, now the lower, end of the primitive streak. A short outgrowth from the gut meets an invagination of the ectoderm. This is evident just at the time that the allantois is forming; and later the walls separating the two processes meet and fuse, thus putting the alimentary canal posteriorly into communication with the amniotic cavity—that is to say, with what will be the exterior. It is then seen that in the chick there is a postanal extension of the gut, and this corresponds with the extension which in reptiles is in communication with the neural canal. This postanal gut degenerates into a solid mass and finally disappears.

The mesoderm during the first day extends outwards as two wings from the notochord and the primitive streak. Like the notochord, it is developed from the endoderm in front and is indeed at first continuous with the notochord. In the region of the primitive streak it is derived from the ectoderm, or rather, as has been seen, from the lips of the blastopore, and forms the mesenchyme of the early yolk-sac vessels. The notochord separates from the endoderm below and contracts into a rounded cord of cells. It is derived, therefore, at the early period of the history of the bird, from the roof of the endoderm. After the tail is folded off, it is continued directly from the cells multiplied at the posterior end of the embryo. These cells form besides in this way the ectoderm, endoderm, and mesoderm, with all of which they are continuous.

In the first day the mesoderm is split into two layers, the somatopleure and splanchnopleure, the former applied to the ectoderm and the latter to the endoderm. The cavity between them is the coelom. The layers remain connected at their outer edge, and again along each side of the notochord. The cavity is thus a closed cavity and, with the fusion which takes place in front of the embryo, the extra-embryonic portion of it forms a cavity completely encircling the embryo.

The formation of the medullary canal is associated with an expansion of the mesoderm on each side, and, beginning anteriorly in the head region, this parachordal mesoderm is split up into a gradually increasing series of myotomes,

connected behind the head by nephrotome necks with the peripheral mesoderm, which latter now encloses the splanchnocoel. In other words, the coelom is resolved into myocoels and a splanchnocoel. In the region of the head the mesoderm on each side of the front end of the notochord may show some transient signs of segmentation, but it appears usually as a mass of unsegmented mesoderm. Behind the auditory organ segmentation is more marked. Seven head segments have been described, but the anterior ones suffer regression, joining the unsegmented mesoderm in front. Finally, only two or three are left to form the tongue musculature supplied by the hypoglossal nerve developed in association with them. With this exception the myotomes are added regularly with growth at the posterior end, and their number is frequently stated to give an idea of the age of the embryo. In the head, also, the region in front of the notochord is supplied with mesoderm by mesenchyme derived from the mesoderm.

These mesodermal rudiments have the fate that we have already observed in other vertebrates. The myotomes yield the skeletal musculature, the dermis, and give off sclerotomes which form the mesenchyme sheaths of the notochord and neural canal. The nephrotomes are from about the third to the fifteenth segment behind the head concerned in the formation of the pronephros and its duct. The pronephros is followed by a mesonephros, and finally by a metanephros. The splanchnocoel, or body cavity, is resolved into the anterior pericardial and the posterior peritoneal cavities.

The mesoderm supplies likewise an abundant mesenchyme which forms the connective tissues and the blood and the blood-vessels. The circulation of the blood in the bird is directed in the first instance to carrying food from the yolk. The vessels arise in the yolk-sac mesoderm and extend into the body as vitelline veins. These approximate behind the gills in the floor of the pharynx to form the heart, and diverge anteriorly to encircle the pharynx, and afterwards the blood is carried to the body by two aortae. From the aortae vitelline arteries arise to connect the system with the vessels of the yolk sac. With the development of the allantois the function of respiration is taken over, leaving the food supply to the yolk sac.

During the incubation of the chick, these vessels are highly developed. The blood to the allantois is carried by special allantoic or umbilical arteries, and the allantoic veins join the vitelline veins.

The limbs are developed as buds of the outer wall and receive derivatives of the myotomes which furnish them with muscles. The forward pair are the wings, the hinder pair the legs.

Towards the end of the period of incubation the yolk sac passes into the body of the chick, and its endoderm is absorbed in that of the intestine. Shortly afterwards the umbilicus closes and the chick pierces the air space at the broad end of the egg and begins to use its lungs. It is hatched by the beak breaking the shell, and leaves behind it the egg together with the allantois, amnion, and the serosa.

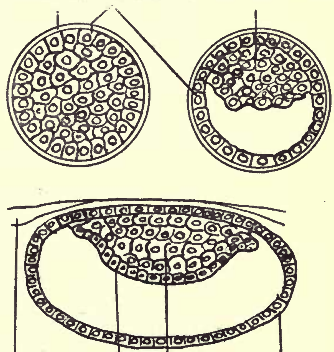


FIG. 126.—Segmentation of the mammalian egg. After van Beneden.

Development of Mammalia.—The eggs of mammals are very small and undergo holoblastic segmentation. This and other modifications are associated with the egg being retained in the oviduct and receiving its food and oxygen from the blood system of the mother. It has become plain, however, from the work of Caldwell, Semon, and of Wilson and Hill, that the lowly oviparous monotreme mammals have meroblastic eggs, and, considered with the marsupials, are in their early stages intermediate between reptiles and placental mammals.

The eggs of the placental mammals measure only 0·1 to 0·2 mm., and, as has been said, are holoblastic in segmentation. The first polar body is liberated before the egg leaves the ovary, and the second after the spermatozoon has entered the egg. It is covered in an egg membrane, the zona radiata, and in the upper part of the oviduct it receives a slight

coating of albumen. Segmentation results in the formation of a ball of cells which differentiates into an outer envelope and a central group of cells. The outer envelope is the serosa, which is early developed to attach the embryo to the uterine wall, and the central cells become cut off from the vegetable pole of the outer layer by a split which is rapidly increased into a cavity distended by a fluid. The central cells remaining attached to the animal pole are resolved into the two

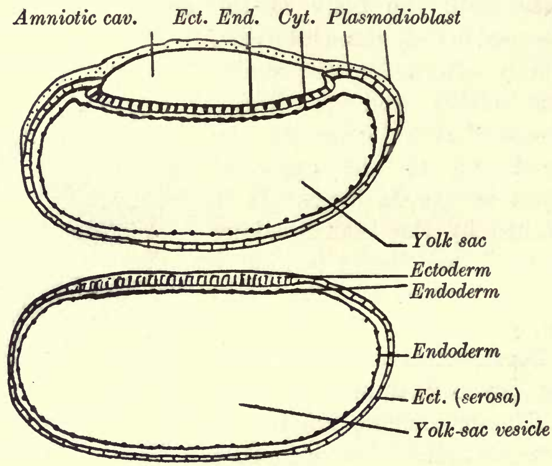


FIG. 127.—Diagrams to illustrate the formation of the primitive amnion of bats, etc. (after van Beneden), and the superficial position of the embryonic ectoderm in rabbits, etc.

layers of the embryonic area. The upper layer is the ectoderm, and it is put into communication with the ectoderm of the serosa; and the lower layer is the endoderm, and at first is restricted to the embryonic area, but soon spreads out by cell multiplication to form a flat layer lining the vesicle. The products of segmentation are thus rapidly resolved into an outer serosa and an embryonic area, or rather, an area pellucida consisting of two layers. Furthermore, the endoderm has grown to the extent to enclose a cavity. The subsequent procedure demonstrates that this cavity comprehends the enteron below the embryonic area and the yolk sac. The cavity above, roofed in by the serosa, is a proamniotic cavity

which in certain mammals, including many rodents, insectivores, bats, monkeys, and man, is retained as the amnion. In others, that part of the serosa which roofs in the embryonic area disappears, and an amnion is developed as in birds and reptiles.

The outer layer, serosa, chorion, or trophoblast, is applied to the wall of the uterus and develops processes which invade the wall. It often becomes double over the embryonic hemisphere or completely, the outer layer of the two thickening to form a plasmodioblast which replaces the epithelium of the uterine wall, and it is invaded by processes of the inner of the two layers, which is formed of cylindrical cells. By this means the maternal vessels are brought into close relationship with the outer part of the serosa, and later the mesoderm brought from the embryo by the allantois invades the processes on the embryonic side. The serosa thus forms the placenta, and it provides for the exchange of food material, and oxygen for waste material, between the two blood systems. In certain rodents the upper part of the serosa is converted into a pouch. These are some of the modifications of the serosa connected with the retention of the embryo in the uterus.

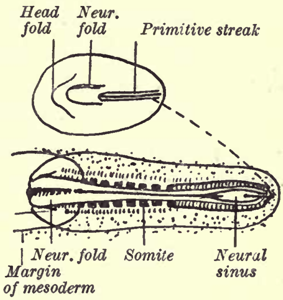


FIG. 128.—Dorsal views of the embryonic area in early mammalian stages (about seven and eight days in the rabbit) to indicate their similarity to those of the bird. Compare with fig. 121.

When these preliminary processes are accomplished the area pellucida, consisting of ectoderm and endoderm, enters upon developmental phases which are similar to those of birds and reptiles. It enlarges, becoming oval in shape and the posterior end pointed. The embryonic area becomes more strictly marked out by a central area of cylindrical cells, and along the mid-line there gradually appears the primitive streak, and, as in the bird, it at once commences forming mesoderm. As in the bird also, it leaves the surface about the middle of the pellucid region and is continued, uniting with

the endoderm as the notochord to a further point in advance. The primitive streak is accompanied by the formation of a primitive groove, and it is continued as a canal at the anterior end of the streak into the notochord. It opens also, sooner or later, into the enteron, and ultimately forms the neurenteric canal. Mesoderm is liberated on each side from the endoderm continuous with the notochord and also with that formed posteriorly by the primitive groove. The neural plate is distinct in front of the streak. The conditions, in short, are directly comparable with those of the bird, still more with those of the reptile.

As has been seen, the blastopore is late in appearing in the case of the chick, and thus evidences the persistence of a process no longer necessary in connexion with gastrulation, but essential in association with postgastrular growth. It is also late in appearance in mammals.

The preblastoporal area of the embryo constantly increases in length, and, as it grows, the structures undergo changes already familiar from the study of the chick.

The neural plate becomes defined by neural ridges which limit the brain in front and extend backwards as folds of the ectoderm. These folds continue to rise and they meet and fuse, leaving a neuropore in front, and extend backwards, fusing as growth proceeds. A neural sinus is left for a time posteriorly, enclosing the front end of the streak. But this is duly roofed over, and the front end of the blastopore is converted into the neurenteric canal.

Head folds are also formed as in the bird, and their formation is accompanied by the head being raised from the area pellucida and the fore-gut being established. The folds are continued backwards, and are met by a tail fold. The enteron is thus converted into fore-, mid-, and hind-gut, the mid-gut still communicating widely with the yolk-sac vesicle. The expansion of the head is accompanied by a mesencephalic flexure, followed by a flexure of the head as a whole. This forms a pit into the area pellucida in front of the embryo, and the two layers—there is no mesoderm at this stage in this region—are carried downwards. In the case of the mammals which form an amnion after the manner of birds and reptiles, the outer wall

of the pit thus formed is met and fused with an amniotic fold which, rising behind the tail and at the sides of the embryo, extends forwards over the embryo. Before this has been completed the allantois has appeared at the posterior end of the enteron and carries the mesoderm out to the wall of the serosa, around which it spreads.

Internally the enteron, more and more defined by the uplift of the embryo and its growth, takes on the features of the adult alimentary canal, with others associated with embryonic life and ancestral history. The stomodeum is developed in front from the ectoderm, and expands inwards to meet with the anterior end of the enteron. It gives off a hypophysis as a dorsal outgrowth which comes into close association with the anterior end of the notochord, and finally is attached to the infundibulum to form the pituitary body. The pharynx is early widened and gives off hyoid and two branchial clefts which grow outwards on each side and are met by corresponding folds of the ectoderm, but the clefts do not become open. The arches are developed between the clefts.

The rest of the alimentary canal is resolved into stomach and intestine, and the glands are formed as outgrowths. Posteriorly the neurenteric canal remains as a communication with the neural canal during the early part of the developmental period. Then it becomes solid and degenerates, leaving for a time a short postanal gut. The proctodeum is formed from the part of the primitive streak which is shut out from the neural canal.

The mesoderm, developed on each side of the notochord and primitive streak, forms a double wing extending outwards from the embryo over the yolk sac. In most cases it does not advance beyond the upper hemisphere of the yolk sac. It is divided into somatopleure and splanchnopleure, enclosing the coelom, remaining joined at the margin and internally in the neighbourhood of the notochord and the primitive streak. The two wings extend forwards, as in the chick, and fuse. The coelom thus extends widely around the embryo. In the case of mammals which preserve the primitive amnion the mesoderm passes into the space between the endoderm and the serosa. As in the chick, the embryos of mammals

which form a secondary amnion have the coelom carried over the embryo in the formation of the amnion.

The mesoderm of the embryo is resolved into myotomes and peripheral mesoderm, the latter enclosing the body cavity. The mesoderm of the head on each side of the notochord forms a mesenchyme except posteriorly, where two or three segments are preserved to form the hypoglossal muscles. The myotomes of the trunk furnish the muscles of the body wall and of the limbs; they also provide the dermis, and from their inner lower border the sclerotomes which yield the mesenchyme sheaths of the notochord and nerve cord.

The myotomes are connected at first by nephrotomes with the splanchnocoel mesoderm. Pronephros, mesonephros, and metanephros are formed in succession, and the history of these will be considered in the next chapter.

The splanchnocoel is resolved in front into the pericardial cavity, and after its separation the lungs extend backwards into dorsal pouches of the pleuroperitoneal cavity. They are thus covered by a visceral layer and surrounded by the parietal layer of the pleura, into the cavity of which they project. They become separated from the peritoneal cavity by the diaphragm, which grows downwards as a fold of mesoderm behind the lungs and the heart. Head cavities do not appear to be formed as such in placental mammals, but they have been found in certain marsupials, and the premandibular cavity yields the oculomotor muscles.[1]

The mesoderm of the yolk sac, mainly that evidently derived from the primitive streak, is the seat of the formation of the first blood vessels and cells. The network is carried inwards towards the body, on each side of which it forms a vessel. With the raising of the body these two vessels are brought into contact to form the heart, and they are enclosed by the pericardium. Diverging in front of the heart the two primitive vessels pass round the pharynx to form the dorsal aortae, from which again vitelline arteries are directed to the yolk sac. The primitive circulation is thus that of the large-yolked eggs of birds and reptiles. The serosa is able to take up an exudate from the uterine wall, and the yolk sac is distended

[1] 1915. Fraser, *Proc. Zool. Soc.*

by a coagulable fluid. The yolk sac in many mammals is brought into close relationship with the blood system of the uterus, a yolk-sac placenta being formed. With the development of the allantois and its spread to form the foetal portion of the placenta, the yolk sac becomes less important, and in some mammals, indeed, it never really reaches the serosa. The allantois mesoderm spreads on the inner side of the serosa, and it at once becomes vascular, establishing a network of

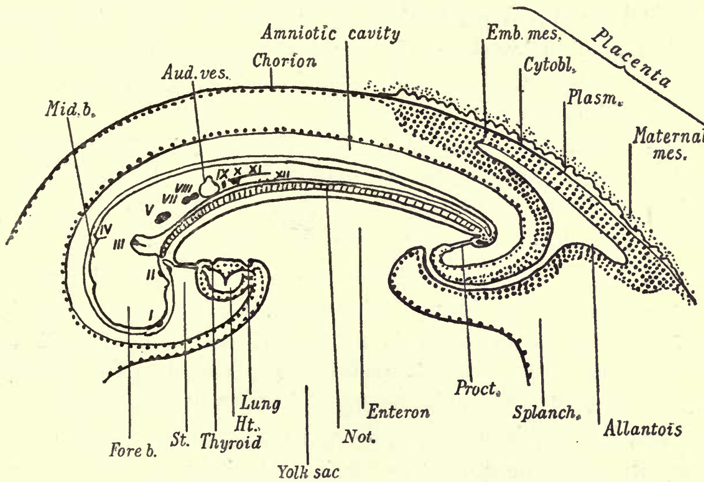


Fig. 129.—Diagrammatic longitudinal section of mammalian embryo (of about ten days in the case of the rabbit).

vessels in the folds of the serosa which are imbedded in the uterine wall. The vitelline veins are reinforced by allantoic veins, and allantoic arteries are developed from the dorsal aorta. The placental circulation is thus introduced, and it forms the means of food and oxygen supply for the rest of the uterine life. It is to be noted that the maternal blood and the foetal circulation are independent, but brought into close relationship in the placenta. The wall between them is the serosa, and it is double over the area involved in placentation. This is a fact of importance, for disease germs of the maternal blood are thus normally shut out from the foetal circulation and only active parasites manage rarely to overcome the barrier.

In its most primitive phase the placenta is a union of serosa and uterine epithelium, and it always starts as such; but in placental mammals the mucous and submucous layers of the uterus are largely replaced by the plasmodium of the serosa. In rare cases the egg fails to enter the oviduct, and after fertilisation grows and establishes its placenta on the peritoneum.

Birth takes place by contractions of the muscular walls of the uterus, the bursting of the amnion and the serosa. The umbilical or navel connexion of the foetus with the serosa and the amnion breaks, or, in cases where help is given, is cut through. The envelopes are detached completely from the uterus as the afterbirth.

The length of gestation is very constant in the different species. It is 30 days in the rabbit, 20 days in the mouse, 56 days in the cat, 62 days in the dog, 340 days in the horse, 280 days in the cow, 140 days in the sheep, and 113 days in the pig. It is probable that a hormone secreted by the foetus gives the signal for birth, but attempts have been made to show that the periodicity is connected with the periodicity of ovulation. The ovary is certainly concerned in the uterine life, for when the ovum is discharged the follicle changes into a corpus luteum if fertilisation takes place. Its growth and persistence may be due to endocrine relationship between the ovary and the uterus, and its presence stimulates the mammary glands to come into function.[1]

CHAPTER XII

MAMMALIA

Phylum VERTEBRATA	
Sub-Phylum CRANIATA	*Type*
Class MAMMALIA	Lepus

THE rabbit is a convenient and easily obtained type for studying mammalian morphology and physiology.

In the wild condition the common rabbit, *Lepus cuniculus*, occupies burrows formed in suitable places and soil. It ventures out from the warren to some extent during the day, but more regularly in the evening, to feed on grass and other herbage, and it appears to have a preference for hard fescue. In the winter, especially when the ground is covered with snow, it may do damage by stripping the bark from trees in plantations and by feeding on crops in fields and gardens. Its burrows also are of importance in certain situations. On the other hand, it is kept under by many carnivorous enemies of the land and the air, and man takes for his uses a large percentage. It is not merely utilised for food, but the skins are valuable and the fur is employed in the making of hats.

Rabbits are liable to the attack of Coccidia, which produce a white-spotted condition of the liver, sometimes mistaken for tubercle. They are the intermediate hosts of *Taenia serrata* and of *Coenurus serialis*.

They reproduce with great rapidity. Several litters are produced by the same doe in a year, and there are five to seven young born each time. The young are born in a blind, helpless condition.[1]

[1] 1898. J. E. Harting, *The Rabbit*. Fur, Feather, and Fin Series.

The description which follows will be found to apply equally well to the other species of Lepus, e.g. the hare, *L. timidus,* the mountain hare, *L. variabilis,* and, indeed, to most mammals.

External Characters.—The rabbit is bilaterally symmetrical and is resolved into head, neck, trunk, and tail, and there are two pairs of limbs; the whole body is covered with hair. The head presents the characteristically long ears. The mouth is bounded by fleshy lips interrupted above by a cleft leading to the nose, a feature which gives mobility to the upper lip and is at the same time a persistent embryonic state. The typical rodent teeth are to be noted; their description will follow. The muzzle is occupied by the paired anterior nares and bears prominent hairs, called vibrissae, which are not merely tactile but are believed to assist in vision. The eye is protected by upper and lower eyelids and a large nictitating membrane which may be pulled over the eye from the inner canthus.

The perineal region is covered by the tail. It presents the anal opening of the intestine and the separate opening for the urinogenital organs. The external appearances are very similar in both sexes, but the female opening will be observed to be a slit forming the vulva on the ventral wall, of which the clitoris is a small conical projection. In the male the penis is only slightly projecting; it is covered by the prepuce, which forms a preputial pouch for its reception. At its base a pair of scrotal sacs form small projections. A pair of bare patches will be observed in both sexes, which are occupied by the orifices of the perineal glands, the secretion of which gives the rabbit its characteristic odour. In the female the ventral aspect of the body is occupied by a series of five pairs of mammary glands, and each is marked by a projecting teat. They are very small in the male.

The limbs have the usual mammalian segments. The fore-limb possesses five digits and the hind-limb four digits, the internal digit being absent. All the digits terminate in horny claws. The hinder limbs, which are the main organs of locomotion, tend to be large in the genus Lepus, and the contrast between the two pairs may be great, as in the jumping hare.

Internal Structure. **Skeleton.**—For the study of the mammalian skeleton it is not necessary nor desirable to select

exclusively that of the rabbit. Almost any mammalian skeleton will answer the purpose, and the bones of the larger mammals are more convenient to handle.

The vertebral column arises in the scleratogenous tissue around the notochord and nerve cord. The connective tissue is chondrified to form centra and arches which constrict the notochord and encircle the spinal cord. The cartilaginous vertebrae are converted into bony vertebrae, centres of ossificaton appearing in the centra and on each side of the arches. Their origin is accompanied by the development of cartilaginous ribs in the septa between the myotomes of the thoracic region, and these are ultimately ossified. The ribs extend around the body, and the anterior ones encircle it, and it is believed that their fusion ventrally forms the sternum. At all events, the sternum is preformed in cartilage and preserves to some extent, and in some mammals to a great extent, its cartilaginous structure through life.

In the adult the vertebral column consists of a large number of vertebrae articulated together to form an elastic support to the trunk and tail. According to the position they occupy, they are resolved into cervical, thoracic (dorsal or costal), lumbar, sacral, caudal. The formula for the rabbit and hare is C. 7, Th. 12 (or 13), L. 7 (or 6), S. 3, Cd. about 15. Comparing the skeletons of other mammals it will be found that the cervical almost always number seven, while the other kinds vary in number. Here are a few examples :

	C.	Th.	L.	S.	Cd.
Horse . .	7	18	6	5	18–20
Cow . .	7	13	6	5	18–20
Sheep . .	7	13	6	4	18
Pig . .	7	14	6	4	20–23
Dog . .	7	13	7	3	18–22
Lion . .	7	13	7	3	19–21
Man . .	7	12	5	5	3-4

A lumbar vertebra consists of a body, or centrum, on the dorsal aspect of which a neural arch encircles the neural canal. It is produced medianly into a neural spine (neuropophysis), and laterally into a pair of large transverse processes. The

articular surfaces are borne on two pairs of articular processes (zygapophyses), anterior and posterior. As in the frog, the posterior processes overlap the anterior, and this holds good universally.

The thoracic vertebrae are different in that the transverse processes are short, and all provide articulation for the ribs. It is for this reason that they are called costal vertebrae. The head of the rib is typically articulated between two centra, each of which therefore bears a half-facet, and the tubercle of the rib to the transverse process of the posterior of the two vertebrae concerned. The spines gradually increase in length from the posterior end of the series, and reach a culmination in the region of the shoulders or withers. In front of this region the spines decrease rapidly in length.

The cervical vertebrae are at once distinguished by their large articular processes and facets, by the vertebrarterial canal, the almost flat spines, and by their relatively large size. The vertebrarterial canal transmits the vertebral artery and is formed by the transverse process above and a rudimentary rib below; the combined process is described as the transverse process. The first two vertebrae are modified to provide rotatory movements of the head. The first, or atlas, is firmly articulated to the skull. It is in the form of a ring which projects widely on each side into transverse processes. It bears on the skull aspect a pair of articular surfaces which are applied to the occipital condyles, and posteriorly a pair of surfaces for articulation with the second vertebra. The ring is crossed transversely by a ligament which divides it into a ventral portion into which the odontoid process of the second vertebra projects, and a dorsal portion which transmits the spinal cord. The axis, or second vertebra, is like its successors posteriorly, but anteriorly the centrum is produced into the odontoid peg, a derivative of the centrum of the first vertebra, which becomes fused with the centrum of the second vertebra. Anterior articular processes are absent. The odontoid process, or dens, is connected by ligaments both with the atlas and the occipital.

The sacral vertebrae are fused into a compact structure which serves to complete the arch formed by the two innominate

bones for the support of the hinder pair of limbs. The centra, the transverse processes, with which rib rudiments are fused, and the articular processes are fused, but the spines are usually left free. The wings of the sacrum provide a pair of surfaces for articulation with the innominates.

The caudal or coccygeal vertebrae, as we follow the series from before backwards, gradually lose their processes and their arches, and finally are reduced to rod-like centra.

The vertebral centra increase in diameter by the action of the periosteum, and in length by the activities of the cartilaginous junction between the body and the flat epiphyses. The increase in size of the arches is provided for similarly by cartilages at their bases. Between the vertebrae are discs of cartilage which allow only of a limited degree of movement, which is assisted by the gliding movements permitted by the articular processes. The vertebrae give attachment to muscles, and are firmly connected by ligaments which are elastic. The tips of the spines are connected by the supraspinous ligaments, and these, when they reach the long spines of the thoracic region, extend forward to be attached to the occipital region of the skull. It thus forms the ligamentum nuchae which serves to support the head, holding it in a horizontal position in front of the body, and a change of this position involves muscular action. Interspinous ligaments unite the successive spines, and a similar flat sheet unites the ligamentum nuchae to the cervical vertebrae. The ligamenta subflava unite the successive arches of the vertebrae, and other ligaments are related to the centra and the articular processes. The articulations of the separate elements of the column thus provide for movement. The movements are very limited in the thoracic region, are more pronounced in the lumbar, still more so in the neck, and especially in the tail. With the exception of the rotatory movements, specially provided between the first two vertebrae, the bending produced by the vertebral column is performed by the co-operation of a succession of vertebrae.

The ribs are preformed in cartilage, and the cartilage is only partially replaced by bone. The ribs are bony above, and are continued downwards in cartilage. In the rabbit the first seven are articulated by their cartilaginous lower extremities

to the sternum, thus forming with their neighbours of the other side complete arches around the body. Such are called sternal ribs. The cartilage portion of the eighth rib fuses with that of the seventh, and the ninth similarly with the eighth. These are termed asternal. The last three (or four sometimes) terminate freely, and such are called free ribs. Similar conditions prevail in other mammals, but as in the horse, for example, free ribs may be absent, all the ribs being attached to one another in succession or to the sternum. The number of thoracic vertebrae corresponds to the number of ribs. Dorsally the ribs are articulated to the vertebral column by the head and the tubercle, and, as has already been noted, the centra of the vertebrae provide half-facets for the head and the transverse processes complete facets for the articular tubercle. This is the typical condition, but it is liable to be departed from, especially posteriorly.

In the rabbit the sternum consists of seven elements or sternebrae. The first extends forward in front of the first pair of ribs as the manubrium or presternum, and the last behind the last pair of ribs expands into a flattened cartilage, the xiphisternum or metasternum. The intervening five elements constitute the mesosternum. It will be found to vary in different mammals with regard to its ossification and the number of its elements.

The thorax is thus enclosed by a framework. The ribs are articulated at both ends, joints being provided which admit of hinge action. From the oblique position of the ribs it will be understood that the width of the thorax is increased when the muscles pull them forwards, and is decreased again after the action of the muscles has ceased. This takes place in respiration.

The skull is introduced during development as a pair of parachordals and a pair of trabeculae. The former fuse, enclosing the head part of the notochord to form the basilar plate; and the latter fuse with the basilar plate and anteriorly to form the ethmoid. The chondrification of the connective tissue around the brain proceeds so as to surround the medulla in the formation of the occipital region, and only a slight distance up each side of the brain in front of this region. The auditory

capsule is also chondrified and the cartilage united with that of the brain case. In front of the brain case chondrification proceeds with the development of the nose. The nose is completely invested in cartilage above, but below is produced into processes bounding the wide foramen of the posterior nares. The nasal capsule provides an opening for the anterior nares, and behind, where it enters into the formation of the orbit, it is perforated by the olfactory nerves. It is divided into two chambers by a septum, and the chambers are modified by the ingrowth of the turbinals, laterally and posteriorly. It is thus evident that behind the nose the cartilaginous skull is widely open, presenting a large fontanelle. It is replaced by the bony skull, cartilage bones being formed by replacement and membrane or covering bones, developed independently.

Visceral arches are produced at the same time. The first or mandibular arch is formed as a Meckel's cartilage, a malleus and incus. The hyoid arch is resolved into a stapes and the anterior cornu of the hyoid. The branchial arches succeed, but disappear with the exception of the first, which persists as the posterior cornu of the hyoid.

The skull of the dog is now commonly used for the study of the adult condition of the skull, but any other convenient skull may be utilised.

The skull is at once resolved into the fused elements, forming the brain case and face, the movable lower jaw, and the hyoid. In section and in superficial view the following bones and their relationship to one another will be easily made out. The frontals form the upper protecting bones of the anterior region of the brain case. They expand into small blunt supraorbital processes, and are bent downwards and inwards to form a large part of the orbit. In section, the frontals are hollow; the cavity called the frontal sinus communicates with the nasal cavity, and is consequently filled with air. The parietals roof a large area of the brain. They take part with the frontals in providing a crest for the upper margin of the temporal muscle, a muscle which runs to the lower jaw. Posteriorly the interparietal is interposed between the parietals. Both the frontals and parietals are membrane bones.

The occipitals and the basal bones of the skull are cartilage

bones. The occipitals are four in number. The supraoccipital is placed at the back of the skull, and it forms the upper margin of the foramen magnum. The exoccipitals are laterally situated, and form the side margins of the foramen magnum. They provide the occipital condyles for articulation with the atlas, are pierced by the condyloid foramen for the twelfth nerve, and are produced into the paramastoid process on each side. The basioccipital completes the foramen magnum and just contributes to the condyles. It extends forward like a

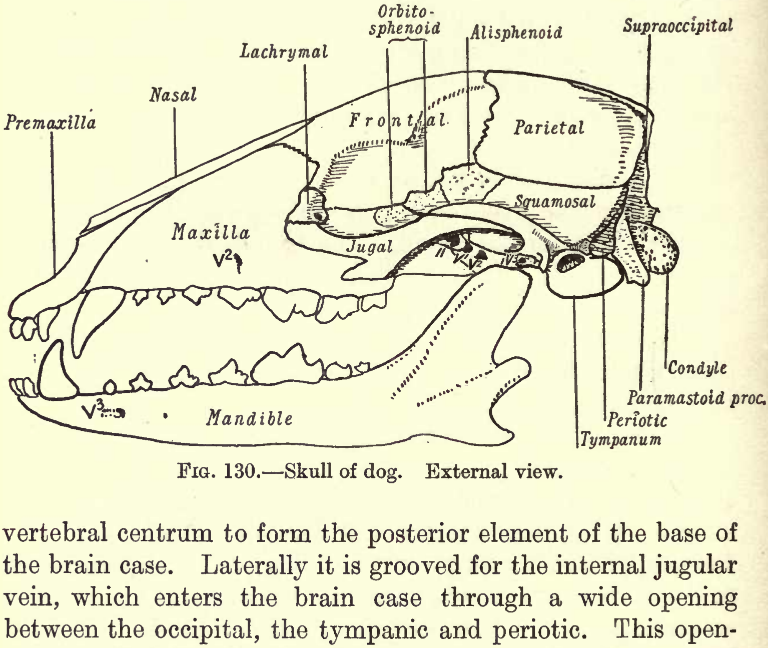


FIG. 130.—Skull of dog. External view.

vertebral centrum to form the posterior element of the base of the brain case. Laterally it is grooved for the internal jugular vein, which enters the brain case through a wide opening between the occipital, the tympanic and periotic. This opening is called the foramen lacerum posterius and transmits also the nerves IX, X, XI.

The sphenoids are six in number, the median basi- and pre-sphenoids and the two pairs of wings, the ali- and orbito-sphenoids. The articulation between the basioccipital and the basisphenoid is along a line joining the front surfaces of the tympanic bones. From this line it extends forward, again centrum-like, to meet the presphenoid. On the cranial surface it bears a depression, the sella turcica, which lodges the pituitary

body, guarded by a posterior prominence, the posterior clinoid process. The presphenoid completes the floor of the brain case, uniting in front with the ethmoid. On the cranial surface it presents a transverse groove for the optic chiasma, and the groove passes into the optic foramen on each side. The alisphenoids are attached on each side of the basisphenoid and come at their outer margins in contact with the parietals and frontals. Each has a descending pterygoid process to support the bone of that name, and each presents two foramina. The posterior is the foramen ovale and transmits

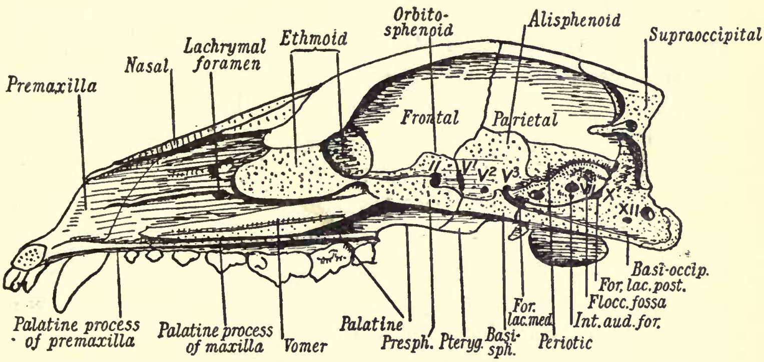


FIG. 131.—Skull of dog. Internal view of longitudinal section. The 'cartilage' bones are dotted, and together give an idea of the embryonic chondrocranium.

the mandibular branch of V. The anterior is the foramen rotundum for the maxillary branch of V. The carotid artery enters the brain through a foramen behind the posterior margin of the alisphenoid: this is the foramen lacerum medium. The orbitosphenoids are similarly fused with the presphenoid and are small wings which come into relationship with the frontals. Between the orbitosphenoid and the alisphenoid is the foramen lacerum anterius—the sphenoidal or anterior orbital fissure—for the ophthalmic branch of V and the motor nerves of the eye, III, IV, VI. The orbitosphenoid is pierced also, as has been observed, by the optic nerve. The maxillary branch of V usually leaves the skull by the sphenoidal fissure, but in the dog it has a separate foramen.

The temporal bone completes the brain case laterally, and it consists of a number of elements. The squamosal is applied to the parietals and alisphenoid, and bears a prominent curved process, the zygoma, which furnishes an articular surface for the lower jaw and articulates distally with the jugal to form the zygomatic arch. It is a membrane bone; so is the tympanic, which forms a widely distended bulla protecting and supporting the drum of the ear. The bulla and the periotic bone bound and form the bony walls of the middle ear, into which the Eustachian tube opens. The outer part of the tympanic supports the beginning of the external passage of the ear. The middle ear is traversed by a series of small bones, the auditory ossicles, which intervene between the drum and the fenestra ovalis of the periotic, and which serve to transmit the sound waves. These have already been mentioned as derivatives of the mandibular and hyoid arches. The malleus is attached by its long process, the manubrium, to the tympanum, and it is articulated to the tympanic bone and to the incus. The incus is articulated to the periotic and the stapes. The stapes is articulated to the incus through the intervention of a small disc, the os orbiculare, and is applied by a broad base to the membrane of the fenestra ovalis (fig. 140). It is perforated by the stapedial artery, a small branch of the carotid. Joints occur between the ossicles, and the ossicles are supported by ligaments. They are cartilage bones. The periotic is a cartilage bone derived from the ossification of the cartilage of the auditory capsule. It is seen only externally, wedged between the squamosal and the exoccipital, but it forms an important element of the inner wall, the so-called petrous portion of the temporal. The inner surface of the bone presents a wedge-shaped ridge for the attachment of the tentorium cerebelli. Below the ridge are the floccular fossa for the floccular lobe of the cerebellum, and the internal auditory foramen for the nerves VII, VIII. The auditory nerve ends in the auditory organ which is lodged in the bone. The facial nerve passes through the periotic, emerges on the inner face of the middle ear, descends close to the stapes and gives off the chorda tympani to the lower jaw, and then comes to the surface of the skull through the stylomastoid foramen between the

tympanic and the paramastoid process of the exoccipital. The outer face of the periotic bone bears the two foramina, fenestra ovalis and fenestra rotunda, the latter being the posterior.

The ethmoid completes the cranium in front. The cribriform plates, perforated for the numerous branches of the olfactory nerve, fill up the space between the sphenoids and the frontals. They meet in a vertical plate. On the cranial side this forms a slight ridge, the crista galli. On the nasal side it forms the nasal septum and extends forwards, supported above by the frontals and nasals and below by the vomer. The lateral masses are attached to the nasal side of the cribriform plates, and will be referred to with the other turbinated bones.

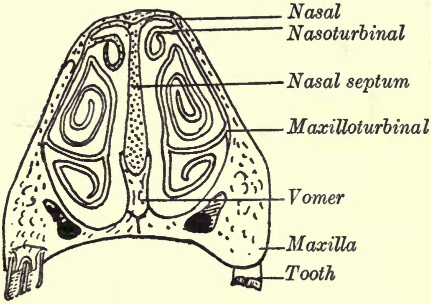


FIG. 132.—Transverse section of nasal region of skull of sheep.

The jugal connects the zygomatic process of the squamosal with the maxilla to form the wide arcade enclosing the temporal and orbital fossae. It also articulates with the small lachrymal which bears the opening for the orbital end of the lachrymal duct. The nasals roof the nose, and the side walls and floor of the nose are formed by the premaxillae and the maxillae. The premaxillae bear the incisor teeth; the suture between the premaxilla and the maxilla lies just in front of the prominent canine tooth; the remaining teeth, the molar teeth, are borne by the maxillae. The palate is formed by the palatine processes of the premaxillae, external to which are the anterior palatine foramina, by the broad palatine processes of the maxillae which meet and fuse in the middle line, and by the palatines. The palatines complete the palate posteriorly, and they also bound the posterior nares. They are associated with the thin vertical pterygoids.

The vomer is the long median bone which extends from the presphenoid, which it embraces by its bifurcated posterior

extremity, to the palatine processes of the premaxillae. It expands posteromedianly into a thin plate, and throughout its length it provides a groove on the upper surface for the reception of the septum nasi.

The nose is bounded by the nasals, maxillaries, and the palatines, and is divided into two chambers by the septum nasi and the vomer. Its outer and posterior walls are occupied by spongy bones developed in cartilage and called turbinals. Posteriorly and fused with the cribriform plate are the lateral masses, the ethmoturbinals. The nasals attach the long nasoturbinals, and the maxillae the large maxilloturbinals. The lachrymal duct opens below the last. The nose is expanded into sinuses which invade the neighbouring bones. The frontal sinuses have been observed. The sphenoid bone is sometimes similarly hollowed, and a large cavity, the maxillary sinus or antrum of Highmore, occurs in the maxilla on each side.

With the exception of the ethmoid and the turbinals all the above bones entering into the formation of the face are membrane bones.

The mandibles are articulated to the squamosal, and both rami are usually separate in front. Each presents above the large coronoid process and posteriorly the articular process and the posterior projection or angle. They bear all the teeth of the lower jaw.

The hyoid consists of a transverse rod, the basihyal, which gives attachment to anterior and posterior cornua. The anterior cornu consists of three bony elements, which from below upwards are the hypo-, cerato-, and stylo-hyal, and after encircling the pharynx with its neighbour it is articulated to the periotic just in front of the styloid foramen. It represents with the stapes the hyoid arch. The posterior cornua, or thyrohyals, are connected with the thyroid cartilage of the larynx and represent the remains of the first branchial arch. They are cartilages and cartilage bones and are seldom preserved in the dried skull.

If other skulls, as that of the horse, are used, differences will be seen, *e.g.* the presence of a foramen in the frontal for the ophthalmic artery and nerve, the uniting of the supraorbital process of the frontal with the zygomatic arch, the foramen

for the ophthalmic and maxillary branches of V occurring in front of the alisphenoid, and that for the mandibular branch of V behind it.

The skeleton of the limbs is preceded with few exceptions in cartilage. The limbs are developed, as in the chick, from a horizontal fold on each side of the body, known as the Wolffian fold. The fold extends from behind the branchial region to the end of the region of the body cavity. The middle part of the fold on each side disappears, and the remaining two parts contract and grow outwards, receiving mesoderm from the somatopleure and muscles from buds of the myotomes. The mesenchyme gives rise to procartilage, and then cartilage. The cartilages are disposed in segments corresponding to the segmentation of the limb, and can be identified as the precursors of the various elements of the skeleton. The cartilages grow with the limb, and later become ossified. The outer layer becomes converted into periosteum and the cartilage is invaded by its outgrowths. The result is that a new circumferential growth takes place, formed by fresh layers derived from the periosteum; and as the bone increases in width it is absorbed internally by cells, called osteoclasts. A marrow cavity is thus formed in the place occupied by the original cartilaginous model of the bone. This process continues during the growing years, and after birth the bone obtains processes by the mechanical conditions of movement and support. At the same time it is growing in length. This is secured by the bones being developed in three portions: the middle part, the shaft or diaphysis, and the two ends or epiphyses. Between these bony elements the cartilage persists and grows, being converted into bone above and below. After growth has been accomplished, the cartilage is finally replaced by bone.

The pectoral girdle of the rabbit consists of a scapula or shoulder-blade and a rudimentary clavicle or collar-bone on each side. The latter is often absent in mammals, but it is preserved in a perfect condition in the Primates, and in similar cases where the movements of the fore-limbs are not reduced to a mere hinge-like state.

The triangular-shaped scapula is suspended by muscles, and is provided with a prominent spine externally associated

with the muscles. The spine culminates in the rabbit in the acromion and metacromion processes, and in other mammals the former at least is usually evident. With it in the perfect condition the clavicle is articulated. The narrow lower extremity of the scapula is occupied by the glenoid cavity, and it is also produced in front into the coracoid process. In the young condition this is a separate cartilage and for a time a separate bone.

The clavicle is a membrane bone, but it is also associated with cartilage, and is thus believed to be a product of the membranous clavicle and the cartilaginous precoracoid. It connects the scapula with the sternum.

The humerus is a long bone and is divided into a shaft and two extremities. The shaft is rounded or columnar in shape, and presents in front a deltoid crest. The upper extremity is rounded and capped with cartilage to enter into the formation of the shoulder-joint with the scapula. Outside this articular area there are the greater and lesser tuberosities separated by the occipital groove. The lower extremity is expanded into lateral condyles and a pulley-like surface divided into two by a ridge. Above the articular surface in front is the coronoid fossa and behind the olecranon fossa. The two may be so deepened as to perforate the bone between them. The coronoid fossa receives the coronoid process of the radius in flexion of the lower limb, and the olecranon fossa the olecranon process of the ulna in extension.

The radius and ulna articulate with the humerus to form the elbow-joint. They are firmly attached, the radius being anterior and medial in position, and the ulna posterior and external.

The carpus consists of a series of small bones which allow of the flexibility of the wrist. With the exception of the sesamoid pisiform, they are cartilage bones. From the medial to the lateral side they are as follows :

Scaphoid (radiale), Semilunar (intermediale), Cuneiform (ulnare),
Pisiform

Centrale (usually absent in adult)

Trapezium	Trapezoid	Magnum	Unciform	
I	II	III	IV–V	carpalia

The metacarpal bones are five in number—and are related to the carpalia as shown above—the medial one being that of the thumb, and the phalanges are the same in number as those of the human hand, viz. 2, 3, 3, 3, 3. The terminal phalanx in each is enclosed in the long horny claw developed from the epidermis, and, like the claw, it is long, tapering, and curved. Sesamoid bones are developed in association with the flexor tendons below the joints of the hand, and may be well seen in the larger skeletons.

The pelvic girdle is formed of two innominate bones which meet ventrally and are united by cartilage, the symphysis, and are separated above by the sacrum. Each innominate consists of (1) the ilium, the forwardly directed element which after articulation with the sacrum expands into a strong gluteal surface and crest. It forms the anterior part of the acetabulum. It is joined there dorsally by (2) the ischium, which extends backwards, forming the ischial crest and spine, and is continued downwards to meet its neighbour below. The acetabulum is completed ventrally by (3) the pubis, which is directed ventrally to meet its neighbour and to fuse with the ischium, thus completing the arch enclosing the obturator foramen. The two pubes in the rabbit are united by cartilage, the joint being called the symphysis pubis. The ischium in many mammals is also involved in the symphysis. In the adult these three bones are firmly fused together, but in the young they are separated, and they are developed independently, remaining connected by cartilage which permits of growth. A small bone is present in this cartilage, the cotyloid bone, and it subsequently fuses with the pubis.

The femur is articulated to the innominate by its projecting rounded head, which fits into the deep cavity of the acetabulum. The upper extremity of the bone is produced externally into the great trochanter. On the ventral aspect of the head there is a smaller process, the lesser trochanter; and further down, in the case of the rabbit, is a third trochanter, a process which it will be observed is well developed on the femur of the horse and its allies. The lower extremity is expanded to form condyles which bear below articular surfaces for the tibia. Between the condyles a groove, the patellar groove, receives

the patella, or knee-cap, and the deep notch below is the intercondyloid fossa.

The patella is the large sesamoid which receives the extensor tendons of the muscles in front of the femur, concentrating their action on the tibia. The intervention of the patella converts the lower part of the tendons into a strong ligament, called the patellar ligament, and it is inserted into the tibia at the tibial crest. Smaller sesamoids may also occur, as in the rabbit, on the posterior aspect of the knee-joint.

The tibia corresponds or is serially homologous to the radius, and the fibula to the ulna. The tibia is the large shin bone and in antero-medial position; the fibula is postero-lateral. The fibula is usually much smaller and, as in the rabbit, fails to reach the knee-joint, and it is more or less fused with the tibia. In the rabbit it articulates by its upper end with the tibia, and below it is fused to it.

The tarsal bones form the ankle-joint. They are as follows:

Astragalus (tibiale-intermediale), Calcaneum (fibulare),
Navicular (centrale)

	Cuneiforms		
First	Second	Third	Cuboid
I	II	III	IV–V tarsalia

The first cuneiform is absent in the rabbit, but a rudiment of it is fused to the second metacarpal. It is absent also in many mammals in association with the absence of the first digit.

There are four metatarsals in such mammals, the first being absent, and the phalanges are three each. When the first digit is present it bears two phalanges. This is the large or inner toe and corresponds serially with the thumb.

The movements are facilitated by the provision of joints between the bones. These may be, as has been observed, merely cartilaginous connexions which permit of a limited degree of movement. More perfect powers of movement are permitted at many joints, as those of the limbs, and in such cases a pad of cartilage is preserved at the opposing ends of the bones, and between them a synovial cavity is developed with a membrane which provides for the surfaces being kept moist.

The bones maintain their relative position by the periosteum being carried across, uniting the two ends, and this, called the capsular ligament, is strengthened in regions where movement is absent or restricted, for many of the joints are hinge joints. The result is that special lateral ligaments are developed. Additional ligaments are provided where necessary, and the whole framework of the skeleton is thus intimately connected by connective tissue, by special ligaments of connective tissue, and by muscles.

Ligaments may therefore be defined as connective-tissue sheets or bands uniting bones together. In some cases they have been derived from muscles which have degenerated.

Muscles are invested in and are divided up by connective tissue, and in the many cases where the muscle is continued into a tendon the connective tissue of the latter is continuous with that which invests and supports the muscle. A tendon therefore is a sheet or band of connective tissue which connects muscle with bone. As we have observed in other cases, the connective tissue is so generally spread throughout the body, connecting the bones, running from the bones to form ligaments and tendons and the sheaths of muscles, that it forms a universal pathway for the blood-vessels and nerves which have also to reach every part of the body.

The skin of a mammal such as the rabbit is formed of a many-layered epidermis based on a connective-tissue dermis. The former is derived from the ectoderm and the latter from the outer layer of the myotomes, and from mesenchyme. The epidermis in section is seen to be resolved into an inner living region called the Malpighian layer, and an outer stratum corneum wherein the cells become flat and horny, thus forming a protection to the other. The external corneal cells are shed constantly, and the layer is being at the same time renewed from the Malpighian layer, and it from the innermost layer. The dermis, true skin, or leather part of the skin is formed of connective tissue and it bears nerves and blood-vessels, both of which penetrate into folds or pits which form papillae at the junction between the dermis and the epidermis. Fat is deposited in the internal part of the dermis.

The function of the skin primarily is to form an elastic,

protective envelope to the body, and in the case of mammals it is characteristically aided in this by the development of hair. Hairs are developed as downgrowths of the ectoderm, into the lower end of which a plug of the dermis is received. It is at first solid, but becomes differentiated into a follicle and the hair. The hair then commences to elongate within the follicle due to the multiplication of cells at the base or bulb, and continues to elongate after it reaches the surface. Associated with the hairs are glands, sebaceous glands and sweat glands.

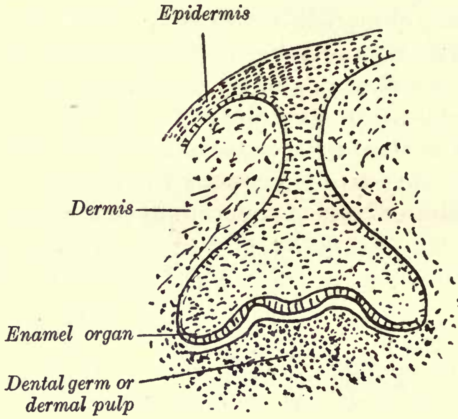


FIG. 133.—A section showing an early stage in the development of a molar tooth.

The former are generally present and distributed all over the skin, but the sweat glands have usually a restricted distribution. The skin also gives rise to mammary glands, but the relationship of the mammary glands to the other two kinds of skin glands is not yet clear.

The epidermis becomes especially modified to form the claws, which grow in each case from their base, and it is from the skin of the mouth that the teeth are produced. During the formation of the gums a dental ridge is formed. From this downgrowths take place at intervals to form the teeth. Each of these expands as the enamel organ. The inner part of this is indented by a dermal pulp. The inner layer of the enamel organ gives rise to the enamel of the tooth, and the

layer of the pulp within gives rise to periosteal-like cells, but called odontoblasts, which proceed in forming an internal lining to the enamel cup of dentine or ivory. The tooth thus proceeds in its growth beneath the gum, and consists of an enamel crown within which is the dentine and within it again the pulp, the last becoming narrower from the activities of the odontoblast layer. When it is erupted the pulp cavity is more and more reduced as the dentine becomes thicker, and gradually it shrinks into a small canal, thus providing for the wear of the teeth. During the years of growth it also continues to add to the length of the tooth. In the case of the rabbit, however, the pulp maintains its position and activity in the lower part of the tooth, and growth proceeds during life from the base, the pulp retreating as the tooth is worn at its free end. The teeth are said to grow from a permanent pulp, and this is the reason that in accidents to the teeth the continued growth brings them into a state which may lead to the death of the animal.

Turning now to the rabbit, the internal structure can be made out by dissection. With the animal fixed to the dissecting board, ventral side upwards, the skin is removed by a median incision and the two flaps reflected. Attention should be directed first to the abdomen, and later to the neck and thorax. The skin is smooth and white on the inner surface. The dermis, as has been noted, is made of connective tissue, and along its ventral aspect the sheet of cutaneous muscle or panniculus carnosus is to be seen, and in the female the mammary glands. It is connected to the muscular body wall generally by connective-tissue strands, but mainly in the region of the limbs. The body wall, in addition to the skin, consists of muscle which forms a thin envelope over the abdomen ventrally and laterally. The bay formed by the ribs in front is occupied by the flat cartilaginous xiphisternum. Between this and the pubis is the median band of connective tissue, the linea alba; and between the ilium and the pubis, Poupart's ligament, which forms an arch through which the nerves and vessels pass to the leg. The external oblique muscle of the abdominal wall runs from above inwards to the linea alba, and a slight incision will demonstrate that it forms a thin sheet, beneath which is

another thin layer, the internal oblique muscle, the fibres of which run in the opposite direction. The longitudinal fibres of the rectus abdominis will also be seen near the medial ventral region of the wall. Continuing the incision, the glistening outer wall of the peritoneum will be seen. A median incision through this along the linea alba, and cuts following the line of the ribs, will expose the abdominal part of the body cavity and its viscera, the nature and relationships of which should be investigated.

The muscles of the thoracic region have their origin in the ribs. The oblique muscles of the abdomen are changed into external and internal intercostals, and from this region spring important muscles, of which the latissimus dorsi and the pectoralis are at once prominent. But it will be better now to describe the organic systems in due order.

Alimentary Canal.—The formula of the teeth of the rabbit, or dental formula, is $\frac{2}{1}\,\frac{0}{0}\,\frac{3}{2}\,\frac{3}{3} = 28$. It means that on each side of the medial line there are two incisors above, one below; no canines; three premolars above, two below; three molars above, three below. It also indicates that the milk teeth of the mammal consist of the first three groups only, viz. the incisors, canines (when such are present), and premolars; the molars are not replaced. The number of the teeth and their arrangement and pattern are of great importance in the classification and the determination of species of mammals. The incisors of the rabbit, as has already been noted, grow from a permanent pulp. The enamel is thick in front, and as the teeth grow and are rubbed against their neighbours of the opposite jaw they are maintained in a sharp chisel-like state.

The grass or other food is nibbled off by the incisors and passed to the molars to be pounded into a pulp. At the same time it is impregnated with the fluid issuing into the mouth from the salivary glands.

There are four pairs of salivary glands. The parotid gland lies just below the external ear, behind the mandible. Its duct, Stenson's duct, runs over the masseter or cheek muscle, and it opens into the mouth opposite the second premolar tooth. Near it is the opening of the duct of the infraorbital

gland, a gland which lies below and in front of the eye. On the inner side of the angle of the jaw is the submaxillary gland, the duct of which, Wharton's duct, runs along the mandible to open into the mouth just in front of the tongue. The sublingual gland lies at the side of the tongue near its anterior end and discharges by several ducts into the mouth in that region.

The saliva is an alkaline fluid containing salines and mucin, and it possesses also the ferment ptyalin which acts upon starch, converting it into maltose. Thus a beginning is made in digestion in the mouth, but the main function is to soak the food and thus help in its mastication and, after that is accomplished, in swallowing it.

The mouth cavity is bounded externally by the lips and the dental arch, between which—that is to say, between the inner wall of the cheek and the gum—lies the narrow space called the vestibule. It is roofed above by the palate, which is resolved in front into the bony palate and posteriorly into the soft palate. The latter ends in the median uvula and the archway leading to the pharynx, and in this archway on each side lies the pit containing the tonsil. The floor of the mouth is occupied by the large muscular tongue, and it is attached to the floor over the greater part of its length, being free only in front. On its upper surface are papillae concerned in the sense of taste.

The pharynx lies behind the mouth and presents also the openings of the posterior nares. Posteriorly it opens below into the windpipe or trachea and above into the oesophagus. The opening into the trachea is guarded by a stiff elastic tongue-like structure which projects upwards behind the tongue. This is the epiglottis. In the act of swallowing, the epiglottis is believed to bend backwards and thus form a bridge over the opening into the trachea, but in several mammals it is evident that the food passes on each side of the projection. When the food is swallowed it is conveyed quickly by peristaltic action to the stomach. The oesophagus passes down the neck dorsal to the trachea, and, traversing the medial plane of the thorax, it pierces the diaphragm, and the tube immediately expands into the stomach. It is lined, like the

mouth, by a stratified epithelium resting on the connective-tissue layer called the submucosa, and its movements are brought about by strong layers of muscle, circular and longitudinal.

The stomach consists of cardiac and pyloric chambers, but is practically a single chamber opening by the cardiac orifice into the oesophagus and by the pyloric orifice into the intestine, the latter opening being on the right side and guarded by a sphincter muscle. The cardiac end of the stomach is lined by a continuation of the stratified epithelium, but in the

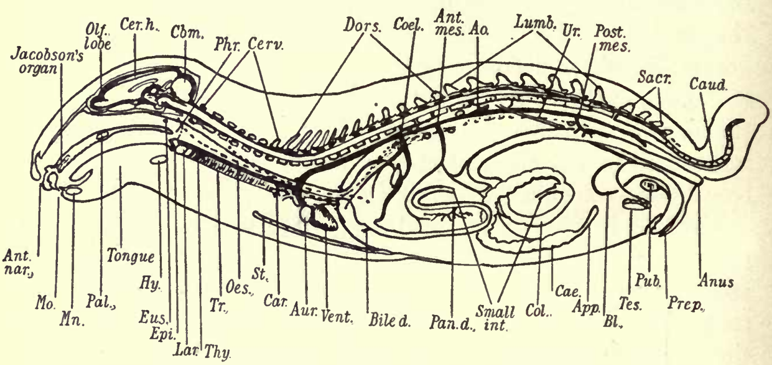


FIG. 134.—General dissection of rabbit to show the relationship of the organs and arteries.
Phr. = pharynx ; *Ur.* = ureter ; *Mn.* = mandible ; *Hy.* = hyoid ; *Epi.* = epiglottis ; *Lar.* = larynx ; *Thy.* = thyroid ; *Tr.* = trachea ; *St.* = sternum.

pyloric region it becomes replaced by a single-layered epithelium which is produced into simple tubular gastric glands. The gastric glands give rise to a fluid which is acid, certain cells of the glands liberating hydrochloric acid, and the fluid contains the ferment pepsin and in the young condition rennin. The alkalinity of the food is not lost all at once, and thus a continuation of the ptyalin digestion may take place for some time. But the action of the pepsin, aided by ferments in the food, the parboiling produced by the heat of the stomach, and the churning action of the walls, splits up the food and reduces it to a more fluid condition containing peptones and liberates much of the material from the mass, and even the cellulose may be split up. It is then passed into the intestine as chyme.

The intestine is resolved broadly into the small intestine and the large intestine. The small intestine is divided up into regions known as the duodenum and ileum. The duodenum is the first loop. It receives the bile duct near its proximal end next the stomach and the pancreatic duct, an exceptional position, near the middle of the far side of the loop.

The liver is a large red gland convex on its outer surface next the diaphragm and fitting into the surface of the stomach and the right kidney on the opposite aspect. It is resolved into right and left lobes and into subdivisions of these. The hepatic ducts combine to form the bile duct, and the right hepatic duct expands on the inner side of the right lobe to form the gall bladder, the duct of which is called the cystic duct. The bile duct then passes to the duodenum. The pancreas is in a simple state. The tubules of the gland lie in the mesentery supporting the two limbs of the duodenum, and the duct opens, as stated, on the distal part of the loop.

The inner wall of the intestine generally is produced into numerous papillae, called villi, and it also invades the submucosa to form many glands. On its walls islands of lymphoid tissue occur, which are termed Peyer's patches.

The upper part of the intestine receives, therefore, in association with the chyme passed from the stomach a supply of bile which brings the food once more into an alkaline condition. Further along the duodenum it obtains the pancreatic juice, and throughout its length it gains the products of the intestinal glands, the secretion of which is called the succus entericus.

The bile has a lubricant action and it is antiseptic. It aids but slightly in the digestion of fats and in converting starch into a soluble state. The pancreatic secretion and the secretion of the intestinal glands play a more active part in digestion. In addition to the mucin, salts and water common to all these secretions of the alimentary canal, these possess important enzymes. Amylase acts upon starch, trypsin upon nitrogenous substances, lipase upon fats. The result of the action of the juices upon the food of the small intestine is to reduce it largely to a soluble condition, from a colloid to a

crystalloid state. Absorption takes place through the villose walls, most of the products passing into the blood, but the fats into the lymphatics, which, from the milky contents after a meal, have been called lacteals.

The undigested residue is passed into the large intestine. The place of entrance of the small intestine is guarded by a valve, the ileo-caecal valve, and at its termination the ileum bears a large accumulation of lymphoid tissue, the sacculus rotundus. The large intestine divides at once into two branches. A blind branch, the caecum, is a long, wide tube spirally constricted and ending in a narrow tube containing a large amount of lymphoid tissue. This is the vermiform appendix, and has the same composition as the sacculus rotundus and Peyer's patches. The other branch of the large intestine is the colon. It is also a wide tube with constricted walls, but it gradually loses the folds and becomes smooth-walled, passing into the rectum, which leads straight back to the anus. It presents the round masses of undigestible residue which are passing to the exterior as egesta or faeces.

The most important substance left over from the digestive activities of the small intestine is cellulose, and it is attacked in the large intestine and especially in the caecum. Time is required for the process, and this is secured in the blind pouch of the intestine, always well developed in animals which feed to a large extent on vegetable food. The process is aided by the heat of the body, the awakening of enzymes present in the food, and to a large extent evidently by the aid of bacteria. The products, together with water and other soluble substances, are absorbed through the mucous membrane of the caecum and colon.

With the exception of the fats, the food, after absorption through the thin mucous membrane of the intestine, is carried to the liver, and it undergoes in passing through the capillaries of the liver some degree of analysis. The carbohydrates are stored in the liver in the insoluble state of glycogen, and only paid out into the blood leaving the liver as required; toxic substances are neutralised. In short, the blood leaving the liver is different from that entering by the portal vein, in so far as food is concerned. In the blood, food is distributed all

over the body ; and in the cells it is used to give rise to energy by oxidation, or it is stored, or converted by further enzymotic action into living protoplasm.

The whole alimentary canal is thus to be looked upon as an apparatus for obtaining and digesting the food so that it can be taken up by the blood and distributed all over the complex body. It is a tube almost entirely made of endoderm, as has been seen from a consideration of the development, and at particular points its walls are provided with glands—that is to say, outgrowths which provide at these points a copious and sufficient supply of the digestive fluids.

Respiratory Organs.—The lungs are the respiratory organs, and with them are associated the windpipe and its branches, and the nose.

The nose is formed as a pair of involutions of the ectoderm, and each becomes connected by a groove with the stomodeum. The stomodeum is indented laterally by the mandibular processes below and the maxillary processes above. The margin of the nasal cavity also becomes prominent in processes, medial and lateral. At this period the conditions are very similar to those illustrated by the skate, a median mass intervening between the two nasal involutions and the mouth being the frontonasal process. The maxillary processes grow medially and fuse in doing so with the lateral nasal processes and then with the medial nasal processes, and fusion is continued internally, with the result that two shelves, palatine processes, grow out which meet and fuse, dividing the nose from the mouth. In cases of incomplete fusion of the upper lip during these changes hare-lip results, and it is usually associated with an incomplete fusion of the palatine processes, thus giving rise to cleft palate.

The two nasal passages thus formed are resolved into two tubes lying between the palate and the brain case. They are lined by a mucous membrane which is ciliated, moist and warm, and is greatly increased in area by the presence of the nasal and maxillary turbinals. The air passes through this labyrinth to reach the pharynx *via* the posterior nares and is filtered from suspended particles. Crossing the pharynx, it is passed into the windpipe and so to the lungs.

The windpipe at its anterior end is modified into the larynx. The upper horseshoe-shaped cartilage is the thyroid, and it supports the epiglottis. The lower circular cartilage is the cricoid. The latter supports on its upper margin two small curved cartilages associated with other two small nodules. These are respectively the arytenoid cartilages, the cartilages of Wrisberg, and the cartilages of Santorini. The arytenoids support the dorsal lips of two folds of the mucous membrane which stretch from the thyroid to them. These are the vocal cords, and the aperture between them may be contracted or expanded by muscles acting upon the arytenoids. The larynx is the organ of the voice. Below it, and embracing the trachea, the thyroid gland will be seen as a red organ expanding on each side into a lobe.

The trachea passes along the neck into the thorax. Its walls are supported by horseshoe-shaped cartilages which keep it distended and elastic. The trachea branches into the two bronchial tubes. In the lung each of these is divided into tubes gradually becoming smaller in diameter. The small branches are termed bronchioles, and they end finally in slightly expanded chambers called alveoli. The cartilages distend the tubes for some distance into the lungs, but they gradually disappear and the walls become thin. In the alveoli the wall is a thin flat epithelium which brings the air into intimate contact with the blood in the capillaries which ramify around them. The oxygen is taken up in exchange for gaseous materials of a waste character, but mainly for carbon dioxide. The oxygen is carried away by the blood loosely united with the respiratory pigment, haemoglobin, lodged in the erythrocytes. It is carried to all parts of the body by the circulation of the blood, and is brought by the capillaries into contact with the living cells doing work at the expense of the energy liberated by the oxidations of fats and carbohydrates brought also by the blood to them.

There is no air in the lungs of the foetus, but at birth the lungs are distended with air. The air contents of the lungs are increased and decreased by the expansion and contraction of the thoracic cavity. The ribs are rotated forwards by the intercostal muscles, and the diaphragm flattened backwards by

the contraction of its muscles. The cavity of the thorax is thereby enlarged, and by the relaxation of the muscles it falls into its condition of rest again. Thus a certain amount of air is introduced during inspiration, and the same amount is expelled during expiration. The air remaining in the lungs after the expiration is called residual air. It is obvious that the quantity of air introduced and expelled depends upon circumstances of rest and running.

Coelom.—The coelomic mesoderm is resolved into dorsal myotomes and splanchnic mesoderm. The former yields the

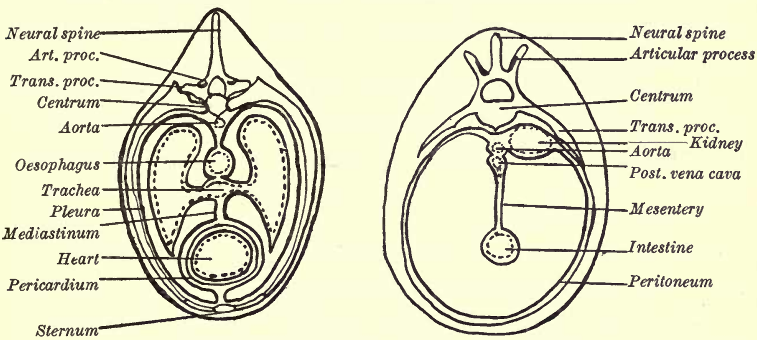


FIG. 135.—Transverse sections through thorax and abdomen—diagrammatic—to illustrate the relationship of the membranes of the body cavities.

muscles of the body and limbs and the dermis. The latter forms the body cavity. The body cavity of the rabbit is resolved into a peritoneal cavity and into pericardial and pleural cavities.

The peritoneal cavity is formed of a parietal layer lining the inner side of the body wall, and it is reflected as a double median fold dorsally to form the mesentery and the investment of the viscera. In the rabbit and other mammals the folding of the intestine is accompanied by a great deal of folding of the mesentery, but throughout it all it maintains its continuity. Anteriorly in relation to the stomach, liver, and diaphragm, the folds of the mesentery are called ligaments and omenta. The inner aspect of the wall of the peritoneum is smooth and it is kept moist. The movements of the

intestine and stomach are thus promoted. The peritoneal cavity is bounded anteriorly by the diaphragm, which completely separates the pleural cavities from the peritoneal cavity. Each pleural sac consists of a parietal layer lining the thorax and its moiety of the diaphragm. In the medial plane it is reflected across the cavity of the thorax in company with its neighbour to the bronchial tubes, where the layers separate to pass in each case along the bronchus and expand to cover the lung. The double membrane formed by the two adposing medial parts of the pleura is called the mediastinum, and in it lie the heart, the important vessels near the heart, the oesophagus, nerves, and other structures of the region (fig. 135).

The pericardium is the similar membrane which surrounds the heart. The inner or visceral layer is firmly attached to the wall of the heart, and the outer or parietal layer leaves the inner layer at the broad anterior end of the heart and comes into close relationship with the mediastinum. The movements of the lungs and heart are thus performed also by the aid of smooth, moist, adposed surfaces.

The rest of the mesoderm is concerned in forming the connective tissues, the blood and blood-circulatory system, and the lymphatic system.

Vascular System.—The blood consists of a fluid, the plasma, in which are present red corpuscles or erythrocytes—in mammals these are not nucleated, the nucleus is absorbed or expelled, or, according to some, the red corpuscles are the liberated nuclei—leucocytes, and thrombocytes. The erythrocytes, as has already been noted, are concerned in respiration. The leucocytes, according to their situation and difference in behaviour, are called by different names ; but they are cells like all blood cells which are free, forming a sort of nomadic tribe outside the direct government of the nerves, though if they be thus outside authority, they are nevertheless the most faithful servants the body possesses. They share in absorbing food which might otherwise fail to reach the blood, and in removing waste. They willingly sacrifice themselves, if necessary, in waging war against all intruders, whether they be living or dead, organic or inorganic. For all these purposes

the leucocytes have a wandering existence among the tissues and accumulate in lymphoid tissue and in lymphatic glands. The thrombocytes, or blood platelets, are directly concerned in the formation of fibrin, and thus occluding vessels when punctured and injured. They form thromboses around intruding objects which penetrate the vessels. The blood of the mammal, like that of the bird, differs from the blood of all other animals, however, in that it is maintained at a relatively constant temperature. It is warm and the temperature varies slightly, according to species. In man the temperature is about 98·4° F. (37° C.), in the rabbit about 102° F. (39° C.), in the horse 100° F. (37·8° C.), in the cow 101° F. (38·3° C.), in the sheep and the pig 103–104° F. (39–40° C.); in the case of birds it is even higher, about 107–108° F. (42° C.). It is evident, therefore, that mammals and birds differ fundamentally from other animals in possessing a mechanism for regulating the gain and loss of heat. The temperature of the lower animals is near to that of the temperature of their surroundings and varies with it, and such are called poikilothermic, or simply cold-blooded. Those animals which maintain a relatively constant temperature independently of their environment are called homoiothermic, or warm-blooded. For one thing, the feathers and the hair contain air next the skin, and the mammal and the bird carry around them a layer of air which is warm and protected from undue loss of heat. The heat, however, is mainly generated by an increase in oxidation, and oxidation is promoted by the increase of the heat. Thus the loss of the heat is prevented by the presence of the body coverings, in the case of aquatic animals by the great thickness of the fatty layer of the skin, and the temperature maintained by the dilatation or constriction of the blood-vessels of the skin. Besides transitory regulation according to circumstances of action, a general change of this nature is an accompaniment of season, the skin being more richly supplied with blood in the summer and less so in the winter. A lowering of temperature means a slowing down of metabolic processes, and in some animals leads to a state of hibernation.

The heart is developed by the approximation and fusion of

the two vitelline veins, as has been described in the case of the chick. It lies medianly below the fore-gut, and in front it diverges to form the first arch, which on reaching the dorsal side runs backwards as the primitive dorsal aorta supplying the embryo and sending the blood back to the placenta or to the yolk sac. The heart expands and becomes constricted into a series of four vesicles which can be identified as sinus venosus, auricle, ventricle, and conus arteriosus. It is also bent into an S-shape. The sinus venosus receives the blood from the yolk sac and the placenta and also from the body of the embryo, and is ultimately absorbed into the wall

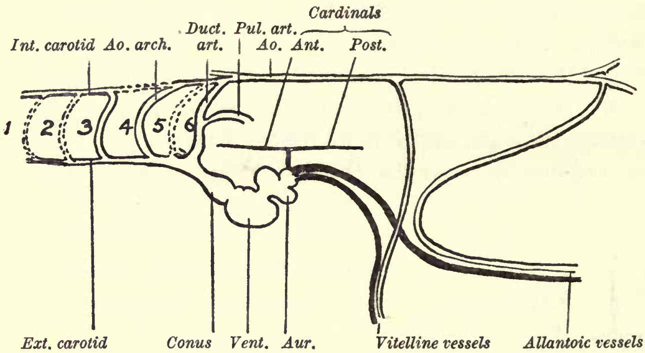


Fig. 136.—Blood circulation of embryo—diagrammatic.

of the right auricle. The originally single auricle becomes divided by a septum which descends across the cavity from the dorsal wall, and fuses with the wall in its descent to the margin of the ventricle. The auricle is thus separated into right and left auricles. The ventricle similarly develops a septum from the apex of the bend which is prominently marked, and this septum grows towards and finally fuses with the auricular septum, thus dividing the ventricular cavity into two separate ventricles, right and left. For a period the auricles remain in communication through a median foramen, the foramen ovale ; and by means of a valve derived from the opening of the sinus venosus, the Eustachian valve, the blood laden with food and oxygen from the placenta and entering the right

auricle by the posterior vena cava is directed through the foramen ovale into the left auricle. While these changes have been taking place the conus has become divided by a septum which separates the vessel into the pulmonary artery related to the right ventricle, and into an aorta opening from the left ventricle. During embryonic life the former maintains its connexion with the dorsal aorta.

The blood, therefore, from the placenta is directed through the foramen ovale into the left auricle, and so to the left ventricle, from which it is despatched to the head. The venous blood of the embryo, brought back mainly by the anterior venae cavae to the right auricle, is sent by the right ventricle to the dorsal aorta by the ductus arteriosus—that is to say, the original remaining part of the pulmonary arch communicating with the dorsal aorta.

At birth, all this is changed; for with the distension of the lungs the blood from the right ventricle is sent to the pulmonary vessels and the ductus arteriosus closes. The foramen ovale is closed, and thereafter the posterior vena cava is concerned entirely with venous blood. Moreover, with the stoppage of the placental circulation, the allantoic vessels atrophy. A circulation is thus established which is that of the adult. The venous blood is received by the right auricle and sent to the right ventricle, and thence to the lungs by the two branches of the pulmonary artery. The arterial blood is brought to the left auricle by the pulmonary veins and sent to the left ventricle, from which it is carried by the aorta to all parts of the body.

The heart may be more conveniently studied by procuring the heart of a sheep. Externally, it may be at once correctly orientated by noting that the apex of the heart is that of the left ventricle, and that the ventral side of the heart is rounded, while the dorsal side is flatter. The outward evidence of the septum separating the ventricles is the sulcus containing the coronary vein, and the ventral one is more conspicuous than the dorsal. The anterior broad end of the heart is occupied by the large blood-vessels and the auricular appendages. If the heart be held, therefore, with the apex downwards and the

ventral side upwards, it will be easy to identify the two auricles and the two ventricles; also to see that the pulmonary artery arises from the base of the right ventricle. Just behind it is the thick elastic aorta. The right auricle will be seen to have passing into it the anterior and posterior venae cavae, and the left auricle the opening of the pulmonary vein.

By opening the right auricle the thin smooth-walled cavity will be found to present the openings of the veins, and also the coronary sinus, a remnant of the left anterior vena cava which receives the coronary veins. In the rabbit the left anterior caval vein persists and the coronary vein opens into it terminally. The auricular appendage presents folded walls due to strands of muscle, called the musculi pectinati. The left auricle is similar in structure and presents the opening of the pulmonary vein. The auricles open by wide apertures into the respective ventricles, and the openings are guarded by valves. These and the ventricular cavities may be best explored by cutting the wall on each side of the septum, carrying the incision from the front to the back of the heart in each case. The valves will be seen to be membranous and attached to the wall of the ventricle by chordae tendineae. The walls of the ventricles are much thicker than those of the auricles, and the wall of the left than that of the right. The internal and external walls of the right ventricle are connected by a muscular moderator band. Internally, the wall is raised into folds by muscular bands, and the chordae tendineae are attached to prominent eminences, called papillary muscles. There are three valves guarding the right auriculo-ventricular aperture, and two that of the left. The former is termed the tricuspid, and the latter the bicuspid, valve. The right ventricle is discharged by the pulmonary artery, and the left ventricle by the aorta. At the base of each of these are three pocket valves with the openings of the pockets directed to the vessel. Each pocket terminates in a margin which is thinner than the rest of the membranous valve, and in the centre of each margin is a hard round body, or nodule, called the corpus Arantii. These valves are termed semilunar valves. In the sinuses formed between the wall of the aorta and two of the pockets are the openings of the two coronary arteries. These

supply the heart wall with blood, and the blood is returned to the right side of the heart by the coronary veins.

The beat of the heart consists in a contraction of the auricles, followed immediately by the contraction of the ventricles. The period of contraction is called the systole, and the relaxation the diastole. After a short pause the auricular systole and the ventricular systole take place again, and are repeated, and it has to be remembered that the contractions begin long before the birth of the animal and cease only with its death. The arrangement of the cavities and the distribution of the blood will be apparent. The auricular systole drives the blood of the auricles into the ventricles, the right receiving the venous blood from the body, and the left the arterial blood from the lungs. The valves between the auricles and ventricles close, and are still more firmly shut during the contraction of the ventricles, thus preventing the blood returning. The contraction of the ventricle opens the semilunar valves, and the blood is discharged into the pulmonary artery on the one hand and into the aorta on the other. The emptying of the auricles and their relaxation is followed by a flow of the blood from the caval veins and from the pulmonary veins. On the other hand, the blood which is sent into the aorta and the pulmonary artery immediately the systole of the ventricles is finished rushes back, but it at once distends the pocket valves at the base of each of these vessels. The nodules, or corpora Arantii, come into apposition and the edges of the valves are firmly knit together. Thus a reflected wave is sent after the primary wave, and these events may be read in the pulse, which indicates in the arteries the successive pulsations of the ventricles.

The circulation of the blood may be followed in the rabbit. The aorta forms an arch on the left side, the corresponding arch of the right side present in the embryo disappearing. Its first branch is the innominate artery, which divides at once into subclavian and carotid arteries, supplying the limb and the neck and head on the right side. As the aorta bends to the left, it yields the left carotid and the left subclavian. Reaching the dorsal part of the mediastinum it sends paired vessels to the thoracic walls, and these are called intercostals.

Phrenic arteries are yielded to the diaphragm just after the vessel has passed through it, and the aorta proceeds onwards along the dorsal wall of the abdomen in the upper part of the mesenteric folds of the peritoneum. It sends off important vessels along the mesentery to supply the alimentary canal and its appendages. The first of these is the coeliac, and it

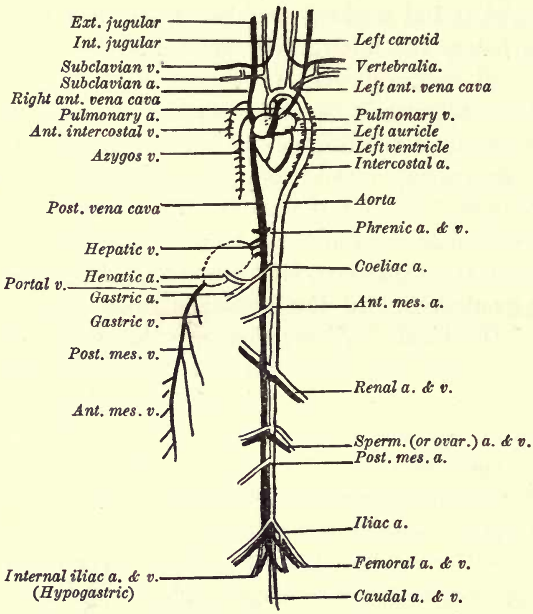


FIG. 137.—Diagram of the blood circulation of the rabbit from the ventral aspect.

divides into hepatic, gastric, splenic, pancreatic, and duodenal branches. The next is the anterior mesenteric, which supplies practically all the remaining part of the intestine. The third is the posterior mesenteric, and it supplies the rectum. These vessels are median and unpaired. Paired vessels are yielded by the aorta to the kidneys—renal arteries—and to the gonads—ovarian or spermatic. Lumbar arteries supply the abdominal walls. The aorta gives off large iliac arteries to the hinder limbs, and terminates in a caudal artery.

The blood carried by these arteries all over the body, and

spread around and in the tissues by capillaries, is reassembled in veins. The veins are thinner-walled than the arteries, and those of the legs are supplied with pocket valves to promote the circulation.

The caudal vein and the veins from the hinder limbs, the iliac and the femoral from each side, combine to form the posterior vena cava, which extends along the dorsal region of the abdomen, receiving lumbar veins, renal and gonadial veins—ovarian or spermatic—hepatic veins, phrenic veins, and then it passes along the mediastinum to open into the right auricle. The blood from the head is returned by large external and small internal jugulars, right and left. These vessels are joined by the right and left subclavians, and in the case of the rabbit the anterior vena cava of each side passes into the right auricle as a separate vessel. In most cases the left vessel formed by the union of the jugulars and the subclavian passes across and joins the right caval vein. The joining vessel is called the innominate vein. The right anterior vena cava receives blood by the azygos vein from the posterior intercostal veins, and by the anterior intercostal vein from the anterior intercostal veins.

The veins arising from the capillaries of the abdominal alimentary canal join together to form the hepatic portal vein, or simply the portal vein. This vessel divides once more into capillaries in the lobules of the liver, and the arterial blood brought by the hepatic artery is mixed with it. The blood of the liver thus derived from two sources is returned to the posterior vena cava by the hepatic veins.

In the capillaries in all regions of the body the blood escapes as a fluid with leucocytes from the vessels and bathes the tissues and organs. The lymph is carried in lymph-vessels, which anastomose to form a highly developed system. In the mesentery the lymph-vessels are especially noteworthy, for there they have had to take a share in the absorption of food. The emulsified fat is conveyed by them, and the lacteals, as they are called, are joined in the upper part of the mesentery by vessels containing lymph from the posterior part of the body. A central median collecting vessel is formed in the anterior region, the thoracic duct, and it discharges into the

left anterior vena cava just below the subclavian vein. The whole system is interrupted by numerous lymphatic glands, and is well supplied with valves directing the flow onwards to the thoracic duct, which is also supplied with valves. The lymph of the left side of the head is received by the thoracic duct, but that of the right side is discharged into the corresponding vein of that side.

Endocrine Organs.—The blood has an important integrating function besides being the means of carrying food, oxygen, and waste products. It is made to convey products which intimate rapidly changes in conditions. The changes undergone by the blood as it circulates are conveyed generally by chemical messages. In addition to messages from one organ to another such as those conveyed take place along the alimentary canal during the digestion of the food, there are special organs which intimate by means of the blood, into which they send small quantities of their internal secretions, hormones, or endocrines, the need for action or a change in growth.

The thymus gland is derived in the embryo from ventral buds of the branchial clefts, mainly from the third. They form in the young rabbit an organ of great size which occupies the mediastinum. It gradually atrophies with age, and is plainly associated with the growing years and in restraining the development of the gonads.

The thyroid, which is developed from the floor of the pharynx, and the history of which has already been explained, yields a proteid body united with iodine, and this secretion has been found to have an important relationship with growth and in promoting the development of sex. If too active it gives rise to exophthalmic goitre; and if atrophied, to the disease myxoedema, cretinism and failure to develop the organs of sex.

The parathyroids are developed from branchials 3 and 4 as dorsal outgrowths, and are usually so closely associated with the thymus as to be difficultly isolated therefrom. They appear to act as neutralisers of the action of the thymus.

The pituitary body, derived from the pituitary outgrowth of the ectoderm of the stomodeum and attached to the infundibulum of the brain, has also important secretions,

derived respectively from its anterior and posterior lobes. It appears to maintain blood pressure, promote growth, and stimulate the secretion of the kidney. If in excess the secretion gives rise to the disease acromegaly and to increased growth ; if it atrophies, to reduced growth and to failure to mature.

The adrenal bodies derived from the mesoderm and the sympathetic system, and situated as prominent yellow bodies anterior to the kidneys, secrete adrenalin, which has the effect of bringing the body to attention in a case of fright by a quick change in blood pressure.

The interstitial tissue of the ovary and testis, with maturity of these organs, gives rise to secretions which develop secondary sex characters, and in certain cases, at all events in aquatic groups of animals, produce migrations. It has been shown also that the fertilised ovum in the uterus gives a special structure to the follicle it occupied in the ovary, and this in turn conveys an intimation to the mammary glands.

The integration produced by the blood conveying messages from one region to another is well preserved in mammals. It is a system which is doubtless even more ancient than the blood, and probably inherited from the circulation of the sap of the mesenchyme spaces.

The spleen lies in the mesentery, close to the stomach, as a large red organ. It is a product of the mesoderm, and acts as a blood reservoir where important changes in the corpuscles take place. In all vertebrates, it may be regarded as providing a reservoir of blood for the liver. The marrow of the bones likewise is concerned with maintaining a supply of red corpuscles and leucocytes. The latter also are derived from lymphoid tissue.

Nervous System.—The neural canal of the embryo, after the closure of the neuropore anteriorly and the neurenteric canal posteriorly, is a closed vesicle. It is expanded in front to form the brain, and the three primary vesicles—the fore-, mid-, and hind-brain—are defined. The hindbrain posteriorly graduates into the condition of the spinal cord. The flexure of the body at its anterior end bends the brain ventrally, and the mesencephalic flexure still further rotates the front end of

the brain underneath the body. The forebrain gives off laterally the paired diverticula, which form the cerebral hemispheres and the paired optic cups. The ventricles of the cerebral hemispheres are the lateral ventricles, and communicate with the original forebrain by the foramina of Monro. The vesicle into which they open is the third ventricle, and this region of the brain is called the thalamencephalon. Posteriorly, this ventricle passes into the cavity of the mesencephalon, and there it is narrowed to form the iter, or aqueduct of Sylvius. The iter passes in turn into the fourth ventricle, which is the cavity of the hindbrain, and it is continuous with the central canal of the spinal cord.

The cerebral hemispheres, or prosencephalon, undergo a great expansion in the rabbit, as in all mammals. Their structure may be followed by dissection and by making transverse sections, and for the purpose it is advisable to obtain the brain of a larger mammal than the rabbit. The brain of the sheep is conveniently obtained, and will be described. It may be found advantageous to get the head of a sheep and study it in longitudinal section. The hemispheres form large paired masses which extend over the median part of the brain, abutting against the cerebellum. The olfactory lobes lie underneath the anterior ends, and the immensely thickened walls are thrown into a series of folds which it will be observed are on the whole paired. Dorsally, the fissura cruciata is marked and divides the frontal from the parietal lobes of the hemisphere. Laterally, the Sylvian fissure separates the frontal and temporal lobes. The surface of each of these lobes is greatly increased in area by the development of grooves called sulci, defining the folds or convolutions called gyri.

On the ventral side the frontal and temporal lobes are limited by the rhinal fissure, internal to which are the olfactory tracts. The most prominent feature of this basal area of the hemisphere is the pyriform area, which extends from the olfactory lobe to the hinder part of the floor.

A median section separating the two hemispheres will show that the separation of the hemispheres is not complete. The two ventricles come close together, and are separated by the

thin adposed walls which form the septum lucidum. The septum expands below into the body of the fornix, and is crossed above by the transverse fibres of the corpus callosum.

Each lateral ventricle extends forwards from the foramen of Monro, and is continued as an anterior horn or cornu, and this is bent downwards to reach the olfactory lobe, becoming reduced in size, and expanding again when it enters the olfactory lobe. The posterior cornu extends backwards and downwards into the temporal lobe. The lateral wall of the anterior cornu is indented by the caudate nucleus of the corpus

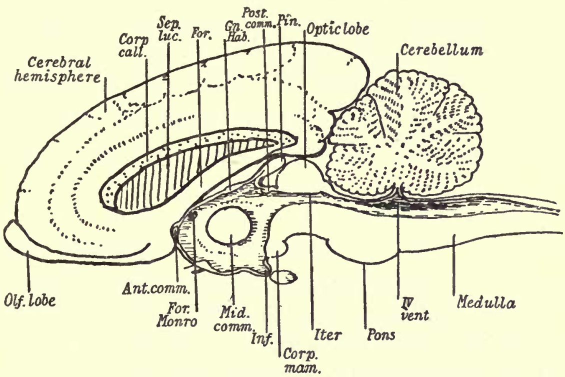


Fig. 138.—Longitudinal section of the brain of the sheep.

striatum, a structure which is completed by the still more external nucleus lenticularis. The hippocampus similarly indents the medial wall of the descending cornu, and follows it in its backward and downward course. It is accompanied by the posterior pillars of the fornix. These pillars are approximated at the mesial end of the hippocampus, and pass forwards as the body of the fornix to diverge close to the anterior commissure to form the anterior pillars which curve round the anterior side of the foramen of Monro and are directed backwards to the corpus mammillare.

Architecturally, the cerebrum is fundamentally that of the lower vertebrate. It is an expansion of, and continuous with, the forebrain and with the rest of the nervous system. But the cerebrum of the mammal is much larger actually and

relatively than that of the lower vertebrate, and during the history of the mammal it has increased in size. The increase has especially affected the free cortex, which has been augmented in area and in thickness. The materials have not been greatly changed, but the number of the units has been multiplied.

This means that mental capability has advanced upon a basis of expansion of the cerebrum, and this is true not only of the history of the Vertebrates as a whole, but also of the classes; not only of the Mammalia, but of the orders into which that class has been resolved.

A section of the hemisphere will show that it is made up superficially of grey matter and internally of white matter. Microscopically, the former consists of nerve cells, the outer of which are pyriform and the inner of the more general multipolar type. In man the pyriform area is the more prominent, and in the lower mammals the deeper types of cells are greater in number. These nerve cells divide into branching processes, called dendrites, and give off each an axon. The grey matter, therefore, is made up of the nerve cells and their dendrites and the proximal and distal ends of the axons, all supported by neuroglia, the connective tissue of the central nervous system. The white matter below is made up of a multitude of axons which connect the cerebral nerve cells with other areas on the other side by commissures, with other parts of the same hemisphere by association fibres between them, and with other parts of the nerve system by sensory or afferent and motor or efferent fibres. The dendrites and the terminal axons are not continuous, but they are close to one another, and these interruptions are called synapses. Experiment has shown also, and pathology has emphasised the fact, that certain parts of the cortex are concerned with special senses, others with association, and that the higher and the more intelligent the mammal, the more do these areas become specialised. But while this is true, it is also true that the whole cerebrum is more or less involved, and works as a whole. The cerebrum, developed phylogenetically and ontogenetically in association with the olfactory sense, has become the centre of all the senses.

The thalamencephalon is formed mainly of the immensely

thickened walls laterally, called the thalami; the thin roof is folded into the velum interpositum, expanded slightly as the corpus habenulare and produced as the pineal body with its stalk. The roof is continued in front into the lamina terminalis, which defines the original front end of the brain. The lamina terminalis passes into the thin floor, which carries the optic chiasma, in front of which is the depression called the optic recess, and behind the tuber cinereum, succeeded by the corpus mammillare and the infundibulum, to which is attached the pituitary body. Anterior and posterior commissures run across the lamina terminalis and the roof respectively, but in addition the side walls meet and fuse, forming the so-called middle commissure. The result is that the cavity of the third ventricle is converted into a ring-shaped vesicle around the region of fusion.

The mesencephalon is roofed by the optic lobes, resolved into the corpora quadrigemina, and the floor and side walls are formed by the thick peduncles, or crura cerebri, which connect the cerebrum with the rest of the central nervous system. The cavity is the iter, or aqueduct of Sylvius.

The hindbrain is resolved into the conspicuous dorsal cerebellum, the transverse commissure of the ventral side, termed the pons Varolii, and the posterior medulla oblongata which passes into the spinal cord.

The cerebellum is a derivative of the extreme forward end of the roof. It grows into a large part of the brain which separates the cerebrum from the hinder part of the skull. Like the cerebrum, it has a cortex of grey matter and a medulla of white matter, and it is folded into lobes separated by fissures, so that in section it has an appearance which has been expressed by the term 'arbor vitae'. The grey matter is divided into an inner layer of multipolar cells, the granular layer, and a superficial layer, the molecular layer, occupied mostly by dendrites. Between them are the conspicuous cells called the cells of Purkinje, which send heavily branching dendrites into the molecular layer. These cells are brought into relationship with the rest of the nervous system by the axons which traverse the white substance from three nuclei and enter the peduncles or brachia. There are three peduncles on each

side : an anterior leading to the crura, a middle to the pons, and a posterior to the medulla and spinal cord. The nerve cells of the cerebellum and their associations with the vestibular centres of the ear have an important function with relation to the sense of position and equilibration ; and the cerebellum is expanded in size in mammals as the centre of muscular movements, of muscle sense and activities in general.

The medulla oblongata is formed of tracts continuous with those of the spinal cord, and is the seat of centres concerned with involuntary movements.

The fourth ventricle is included between the medulla and the cerebellum. It is surrounded by the thick walls of the medulla and has a thin roof below the cerebellum.

The brain is covered by the pia mater, which leads blood-vessels into the walls. Vessels are carried in at the velum interpositum and the fourth ventricle, forming in each case a choroid plexus. The skull is lined by the dura mater carrying the meningeal vessels, and between the two layers is the arachnoid space containing a watery fluid and lined by a delicate inner and outer membrane and extending the length of the brain and spinal cord.

The cranial nerves are described as twelve in number. The olfactory is associated, however, with a nervus terminalis.

I. olfactory ; sensory, olfactory lobe, numerous branches passing through the cribriform plate to reach the sensory cells of the nasal epithelium.

II. optic ; sensory, optic lobes, thalami and cerebrum. The fibres forming the optic tract decussate in the optic chiasma, and the optic nerves pass into the respective orbits through the optic foramen, enter the eye and expand into the retina.

III. oculomotor ; motor, floor of mesencephalon, leaves the skull by the foramen lacerum anterius, and supplies the superior, internal, inferior recti, and the inferior oblique muscles of the eye.

IV. trochlear ; motor, decussates on the roof of the brain just behind the optic lobes, and each nerve leaves by the same foramen as the previous one, supplies the superior oblique muscle of the eye.

V. trigeminal ; mixed, anterior end of medulla, originates

in a Gasserian ganglion connected with the brain on the one hand and the periphery on the other, divides into the sensory ophthalmic which leaves the skull by the foramen lacerum anterius, supplies the skin of the nose and upper parts of the orbit and the muzzle. The sensory maxillary also leaves by the foramen lacerum anterius, and is directed in palatine branches to the palate and in a dental nerve to the teeth of the upper jaw and to the skin of the face. The mixed mandibular leaves by the foramen lacerum medium, and supplies the muscles of the lower jaw, the tongue, and the teeth of the lower jaw.

VI. abducent; motor, floor of medulla, leaves the skull by the foramen lacerum anterius, and supplies the external rectus muscle of the eye.

VII. facial; mixed, forms the geniculate or facialis ganglion, leaves the cranial cavity by the internal auditory foramen, and, gaining the middle ear, passes out by the stylo-mastoid foramen. It is originally the nerve of the hyoid cleft. It gives off in succession the chorda tympani which unites with the lingual branch of V, the palatine to the palate and the floor of the nose, uniting with the maxillary branch of V, and a hyomandibular distributer to the muscles of the face and the external region of the mandible and to the hyoid.

VIII. auditory; sensory, with auditory ganglion leaves by the internal auditory foramen and divides into cochlear and vestibular branches in the internal ear.

IX. glossopharyngeal; mixed, forms a ganglion, leaves the skull by the foramen lacerum posterius. It is originally the nerve of the first branchial cleft, and supplies the tongue and pharynx.

X. vagus or pneumogastric; mixed, forms a ganglion, leaves the skull with IX. It is the nerve of the remaining branchial clefts in the embryo. In the adult, it is distributed in succession by branches: (1) the superior laryngeal to the muscles of the larynx, (2) a nerve which descends the neck to supply the heart, lungs, and stomach. It is accompanied by (3) the depressor nerve of the heart, and at the level of the heart (4) the recurrent laryngeal leaves the main nerve, that of the right passing under the innominate artery, that of the left under the aortic arch. It ascends along the trachea to

reach the larynx, where it supplies most of the muscles. The peculiarity of distribution is explained by the fact that the heart is developed far forwards and the posterior nerve of the larynx lies behind the vessels named. As the heart is carried posteriorly into its adult position, the nerve retreats with it.

XI. accessory; motor, is derived from the dorsal neural crest behind the vagus and in association with the vagus. It arises from the side of the upper part of the spinal cord and

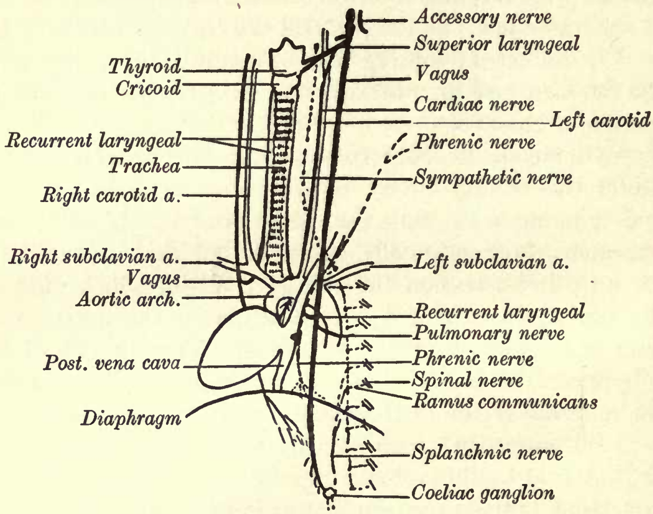


FIG. 139.—A diagram of the nerves of the neck and thorax.

from the side wall of the medulla, and leaves the skull with IX and X. It is supplied to the sternomastoid muscle and the trapezius muscle.

XII. hypoglossal; motor, from floor of medulla, leaves the skull by the condylar foramen and supplies the muscles of the tongue, and by a descending branch the sternothyroid and sternohyoid muscles.

The spinal cord extends from the medulla along the tunnel formed by the neural arches of the vertebrae to the lumbar region, where it ends in a thin prolongation formed by the meninges and called the filum terminale. It is almost completely divided into lateral halves by the deep dorsal and

ventral fissures, which nearly reach to the central canal. The grey matter is central, and in section appears as dorsal and ventral horns on each side. This contains the nerve cells, and the axons forming the white superficial matter are arranged in longitudinal tracts. The spinal nerves arise in dorsal and ventral roots, which are united to form a common nerve. The dorsal root bears a ganglion in each case, is sensory, and is connected to the dorsal horn; the ventral root does not bear a ganglion, is motor, and arises from the ventral horn. The former is afferent, and the latter efferent. The spinal nerves innervate the skin and wall of the body, and through the sympathetic system are also related by sensory and motor fibres to the viscera. Thus simple nervous impulses affecting the body alone may be conducted without reference to the brain—that is, without consciousness.

The first spinal nerve is situated between the skull and the first vertebra, and the succeeding nerves come out in front of the corresponding vertebrae. With the exception that there are eight cervical spinal nerves, the numbers agree with the numbers of the vertebrae. The brachial plexus is formed by the association of the spinal nerves from the fifth cervical to the first thoracic, and it supplies the shoulder and the fore-limb. The fourth cervical, with branches from the fifth and often the sixth, sends a phrenic branch to the diaphragm. It runs along the anterior and posterior venae cavae to reach its destination. The fifth, sixth, and seventh lumbar nerves and the sacral nerves combine to form the lumbosacral plexus, yielding the crural, obturator, and the sciatic nerves to the gluteal region and the leg. They are succeeded by the caudal nerves, which are carried backwards from the end of the cord to pass out in succession between the caudal vertebrae.

The sympathetic nervous system consists of a chain of ganglia developed from the spinal ganglia and forming two longitudinal strands which extend from the cranial nerves V, IX, and X to the hinder part of the body. In the neck are anterior and posterior cervical ganglia, and thereafter ganglia corresponding to each spinal nerve, with which each ganglion is connected by a ramus communicans. The ganglia consist of multipolar cells and distribute impulses to the heart, vessels,

and viscera. The thoracic ganglia give rise to an important nerve, the great splanchnic, which pierces the diaphragm and meets branches coming from the gastric branch of the vagus to form a ganglion situated in the mesentery between the coeliac and anterior mesenteric arteries. This is called the coeliac ganglion. The coeliac ganglion is connected with the anterior mesenteric ganglion placed just behind the artery of that name, and again with a posterior mesenteric ganglion lying just in front of the posterior mesenteric artery. The involuntary muscles of the viscera, the adrenals, and other organs are supplied by the innumerable branching fibres of a system which unites cranial and spinal nerves with an efficient distributing system (fig. 139).

The complex body of the mammal is thus under the control of a nervous system which brings every part into relationship with the rest, and the system is perfected by chemical integration of endocrines. In addition, the animal is brought into relationship with its environment by afferent nerves which are distributed to the skin and to special organs which have been formed from the skin. These are the special sense organs.

Sense Organs.—The olfactory organ is situated in the internal part of the nose. The epithelium is spread and extended over the labyrinth provided by the foldings of the ethmoturbinal. It consists of columnar cells supporting the sense cells. The sense cells are spindle-shaped, the free end terminating in a process lying in the mucus which covers the surface, and the other continued as the olfactory fibril to the olfactory lobe of the brain. It acts as a receptor of chemical products carried by the air, and is thus closely associated with taste.

The eye, broadly speaking, is essentially that of the fish and of the amphibian, but it is refined in structure, and it is brought into important relationships with other centres in the nerve endings in the cerebrum. Anatomically, it has the structure which has already been described (p. 179). The retina is the essential receptor organ, and is formed of rods and cones directed to the back of the eye. On the other side—that is to say, between them and the rays of light—they are related to nerve cells, and through the cells to nerves which run together

to form the optic nerve. It is believed that the retina is acted upon photochemically, undergoing also pigment change and electrical changes.

The auditory organ, the only remaining element of the acustico-lateralis system of organs, has already been explained so far as the middle and external regions are concerned. The internal labyrinth presents the usual three semicircular canals, a utriculus and a sacculus, but from the last the cochlea has

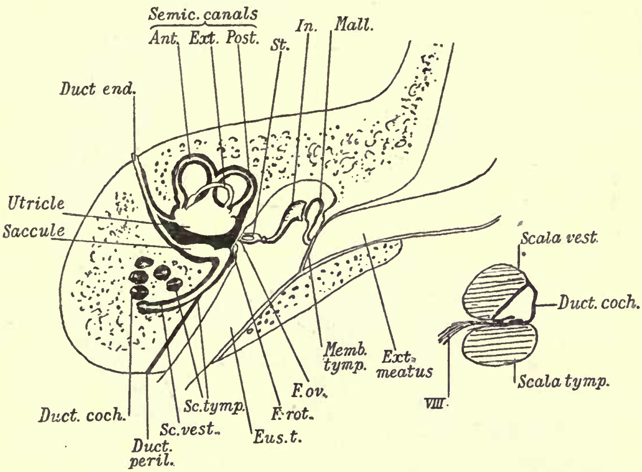
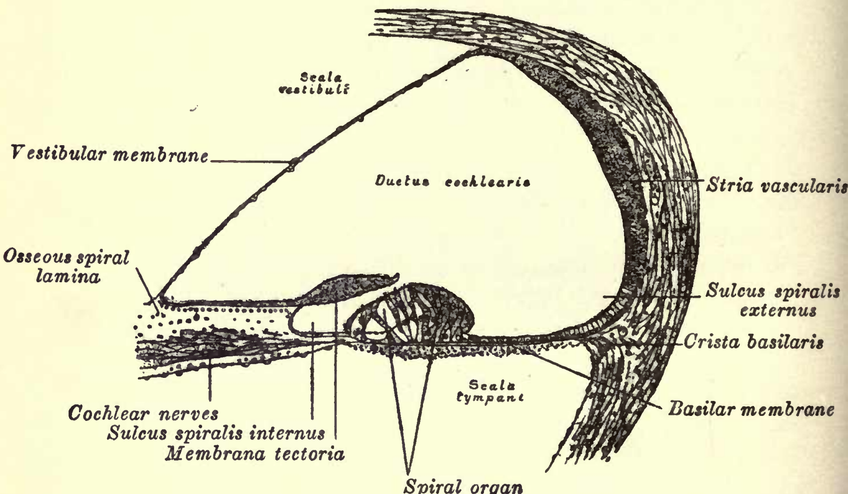


FIG. 140.—General diagram of the auditory organ, and to the right a magnified view of a section of the cochlea.

grown out as an important organ in the form of a coiled tube. The whole organ is closed and is kept distended by endolymph from the ductus endolymphaticus. It is embedded in the periotic bone, from which it is separated by perilymph. The cochlea, however, is attached to the wall of the canal in which it is placed throughout its length. It is applied to one face of the canal, and it is drawn to an angle opposite to this to be attached to a shelf which projects from that side of the canal. The effect of this is to divide the bony canal into three canals, the middle one of which is the cochlear duct, the other two containing perilymph. In the cochlear region, therefore, the perilymph is separated by the cochlear duct, and the two

channels communicate at the distal end of the cochlea. At the proximal end one of these perilymph canals opens on the upper or vestibular side, and is called the scala vestibuli; the other opens on the ventral side near to the fenestra rotunda, and is called the scala tympani. The cochlear duct is often termed the scala media. It is in section a triangular-shaped sac. One limb of the triangle is applied, as has been said, to



(*From 'Gray's Anatomy.'*)

FIG. 141.—A still more magnified view of the cochlea to indicate details of structure of the organ of Corti.

the bony side of the canal; the upper side is bathed externally by the fluid of the scala vestibuli, and the lower limb by that of the scala tympani. These free membranes meet and are supported by the shelf or spiral lamina. Between the spiral lamina and the wall the lower membranous part of the cochlea has been greatly modified, forming the organ of Corti, and it is supplied by the branches of the cochlear nerve. The organ of Corti consists of sensory cells ending in hairs and divided into a row of single cells internally, and a row of three or four cells externally, by two stiff supporting cells, called the rods of Corti, and all based on an elastic fibrous layer, the basilar

membrane. An elastic membranous projection from the lamina spiralis covers them and ends freely over them: this is the membrana tectoria. The waves coming to the perilymph by the fenestra ovalis are distributed as waves of condensation and rarefaction, quadrupled in velocity and increased some thirty times in force in that fluid, and are passed into similar waves of the endolymph. The function of the fenestra rotunda is to act as a disperser of the waves.

The auditory organ is divided, therefore, into a vestibular portion supplied by the vestibular nerve, and a cochlear portion supplied by the cochlear nerve. The former is the primitive part of the organ and is relegated to equilibration. The semicircular canals are directed mutually at right angles. They are each furnished with an ampulla in which sensory cells are developed with stiff hairs which are affected by changes in the flow of the endolymph, and these are associated with similar areas in the utricle and vestibule.

The cochlea is the part of the auditory organ associated with hearing, and especially with the fine distinction of sound waves; and it is evident that the hair cells of the organ of Corti, are the sensory elements developed for the purpose. They are very numerous along the length of the organ and, as has been said, they are supported upon an elastic membrane the fibres of which radiate from the lamina spiralis to the opposite wall. The cochlea differs from the rest of the labyrinth in that it is firmly attached to the wall of the chamber on each side. The free borders of the vesicle are placed at about an angle of 60° with one another. Both are taut, and the lower one, bearing the organ of Corti, is still further stiffened by the lamina spiralis and by having a thicker wall. The sound waves of condensation and rarefaction are sent down the scala vestibuli and up the scala tympani and will affect both membranes, the one after the other. This means that the wave is reconverted into a wave of vibration which is communicated to the endolymph, and so to the hairs of the sensory cells. If the sound is to be analysed according to the waves it produces, it follows that the cells either have a selective power or are affected according to the position of nodes and internodes. A wave received from the scala

vestibuli and communicated to the endolymph might be supposed to affect the membrana tectoria, and by depressing it at a given spot, or spots, produce the result. A wave from the scala tympani might be supposed to have a similar but direct effect by raising a particular region of the organ against the membrana tectoria. As the length of the fibres forming the basis of the organ of Corti gradually increases from the base to the apex, it has been assumed that as these are fixed at both ends they will vibrate only in relationship to waves of a particular pitch, and that they are therefore the mechanical means of communicating to particular cells a given wave. In other words, the drum and the membrane of the fenestra ovalis are aperiodic and communicate all kinds of waves indifferently; the basilar membrane is periodic in gradually changing degree from one end to the other. This is the basis of Helmholtz's theory of hearing. Wrightson's is founded on the action of the nodes and internodes produced by the resonance of the basilar membrane as a whole. It is possible that the membrana tectoria has the effect of directing the wave of the endolymph across the fibres, and primarily and perhaps even in its highest state of development, in the human ear, the endolymph is the means of communicating the sound waves to the sensory cells. It is certain, at all events, that the cochlea is the organ of hearing, that injury to it produces deafness, and that the organ of Corti elaborates for the nervous system the sound waves.

The mammalian nervous system is in a high state of development. But it does not differ from that of the other Craniates except in quantity and quality. Broadly, it may be resolved into somatic receptive constituents, including the distant receptors—the sense organs, the nose, eye, and ear—the cutaneous nerves and centres associated with these in the central nervous system, and the paths which bring them into relationship; visceral receptive, which bring to the central nervous system impulses from the viscera by VII, IX, X; somatic effective, the motor nerves of the brain and spinal cord; visceral effective, afferent fibres of V, VII, IX, X, XI, and visceral motor fibres of the spinal cord distributed by the sympathetic system.

Urinogenital Organs.—The pronephros of mammals is a rudimentary formation of the nephrotomes of about the fourth to the eleventh mesodermal somites of the body. The pronephric tubules fuse to form a solid mass which grows backwards as the pronephric duct, and this fuses in turn with the cloaca. The duct becomes hollow, but the pronephros gradually disappears.

The mesonephros is formed in the solid and fused products of the nephrotomes of succeeding segments. From this nephrogenous tissue the segmental tubules arise on the medial side of the pronephric duct. At first solid, the tubules become hollow and open at one end into the pronephric duct, and each at the other end expands into a Bowman's capsule which becomes indented by a glomerulus of a branch from the aorta. The tubules undergo growth and convolution, and secondary and tertiary tubules arise from them as outgrowths. The mesonephros thus forms a conspicuous organ in development, but, following the degeneration of the pronephros, a number of the anterior tubules of the mesonephros disappear even before the posterior ones have been formed. The duct is the pronephric duct, but it may now be termed the mesonephric or Wolffian duct, and it opens, as has been stated, into the cloaca.

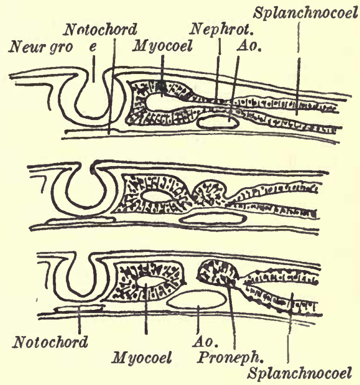


Fig. 142.—Transverse sections to illustrate the development of the pronephros.

The metanephros, the definite kidney of the mammal, arises as a tubular outgrowth of the mesonephric duct. The tube springs from the lower end of the duct on its dorsal side and grows forward. Distally, it dilates and is produced into a series of kidney tubules which come into relationship with the mesoderm, and a compact organ if formed. The blind ends of the tubules form Bowman's

capsules and each receives a glomerulus. The original duct is the ureter.

The germ cells appear in a genital ridge formed medially to the mesonephros. The peritoneal epithelium becomes infolded, carrying with it the germ cells. In the case of the male these form the tubules of the testis, and they become connected with a number of the mesonephric tubules. The tubules of the testis thus open into the mesonephros, which is

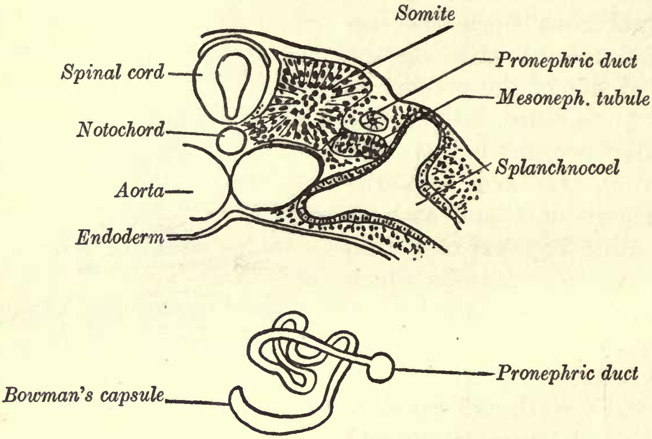


FIG. 143.—Transverse section of a more advanced stage through a developing mesonephric tubule, and (below) a diagram of a mesonephric tubule at a later stage.

the Wolffian body or epididymis, and the mesonephric duct or Wolffian duct becomes the vas deferens. The ducts connecting the epididymis with the testis are called the vasa efferentia.

In the female, the corresponding foldings of the germinal ridge form the follicles containing the ova. The duct is a special formation. In front of the mesonephros a thickening of the peritoneum develops a groove which forms an opening into the peritoneal cavity and, fusing posteriorly, grows backwards close to the Wolffian duct. This is the oviduct or Müllerian duct. The anterior internal opening becomes the internal opening of the Fallopian tube, and the duct forms the Fallopian tube and the uterus. It fuses with its neighbour caudally,

thus producing usually a median part of the uterus and also the vagina.

In the meantime the Wolffian duct and the ureter have been separated, the ureter remaining connected with that part of the cloaca which contributes with the upper end of the allantois to form the bladder. The Wolffian duct and the Müllerian duct at their posterior ends open into the cloaca.

According to sex, the after-development is accompanied by a degeneration, in the case of the male, of the Müllerian duct, and in the case of the female of the Wolffian duct. The terminal end of the intestine is shut out from the cloaca, which is thus resolved into the anus and the urinogenital canal.

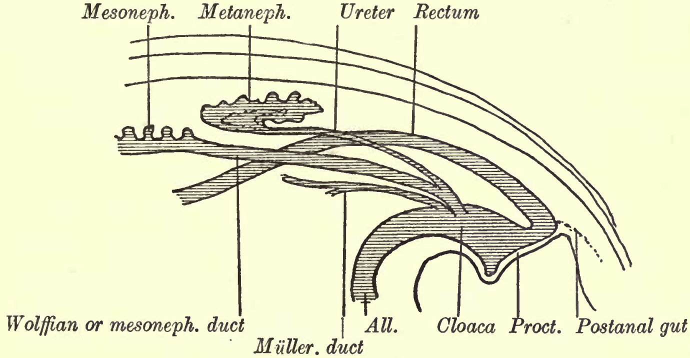


FIG. 144.—The embryonic condition of the ducts at the posterior end of the body.

At first the urinogenital canal is similar in both sexes, but, as development proceeds, folds appear on each side of the opening. These form the vulva of the female, and fuse in the male to form the scrotal sacs, and the canal in the male is further produced by the development of the penis. The penis is also formed on the anterior side of the vulva of the female as the clitoris, but remains small.

It will not be difficult with this explanation to understand the conditions which may be followed in a dissection of the rabbit. The kidneys are situated one on each side of the abdomen. They are covered by the peritoneum. Each has the typical kidney shape. Sections show that they are made up

of a mass of tubules which, beginning in Bowman's capsules in the cortex and fusing with other tubules, end in a cavity termed the pelvis of the kidney. The renal artery gives rise to branches which form glomeruli tufts of capillaries in the glomerular organs, and the efferent vessel splits once more into capillaries around the proximal end of the tubule. A head of water is thus provided at the beginning of each tubule, and the waste material is removed from the blood by the cells of the tubules. The waste consists of organic material as urea

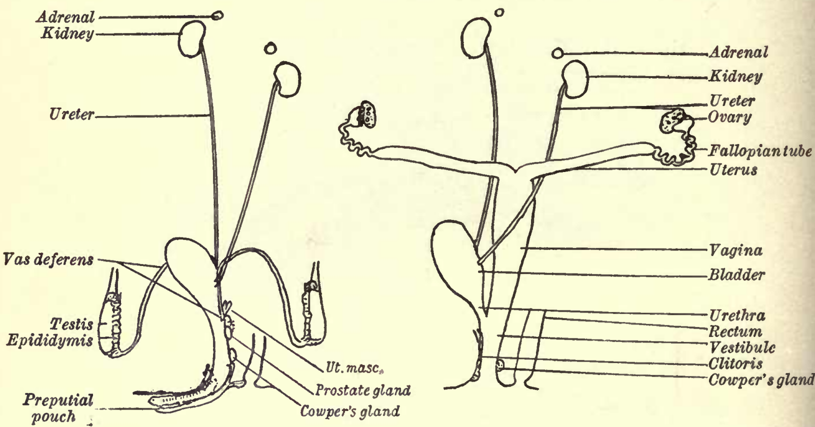


Fig. 145.—Male and female reproductive organs of the rabbit.

and uric acid, with carbonates and other salines. These are carried down the tubules in a state of solution as urine to the pelvis of the kidney. From this the ureter springs on the indented inner border or hilum of the kidney, and the two ureters open near each other on the postero-dorsal wall of the bladder.

In the male, the testes originally formed on the dorsal wall of the peritoneal cavity are carried with the fold of peritoneum which covers them posteriorly to the scrotal sacs, where the cavity is lined by the peritoneum, now called the tunica vaginalis. The testis on each side is an elongated white body. Anteriorly it is connected by the vasa efferentia with the epididymis. The epididymis consists of the coiled tubes of the Wolffian body and leads posteriorly into the vas deferens.

Each vas deferens leaves the scrotal sac at its proximal end, together with the artery and the vein and the cremaster muscle, and is directed to the dorsal side of the bladder, where it gains the medial space on the dorsal side by passing between the bladder and the ureter. In this space the two vasa deferentia descend to open side by side on the dorsal wall of the urinogenital canal or urethra. They open on an eminence called the verumontanum, and on each side of this are the many openings of the prostate gland; still further down are the openings of Cowper's glands. Beyond this, the urethra is embedded in the vascular corpus spongiosum flanked by the two adpressed corpora cavernosa. The latter are attached by the erector muscles to the ischia, and the former expands at the anterior end to form the glans. The glans bears the external opening of the urethra. It is covered with the free part of the penis by a skin, the inner layer of the glandular preputial pouch.

In the female the ovaries lie on each side of the peritoneal cavity. They are oval in shape, and the distended follicles project from the whitish surface or are visible as clear spots. Each follicle contains an ovum, and the ova are liberated at periods of ovulation. They are received by the wide opening of the Fallopian tube which lies close to the ovary on each side. The Fallopian tube is a narrow tube which, after a slight degree of convolution, expands to form the uterus. The two uteri approximate and join, but do not completely fuse medially, each opening by an os uteri into the median vagina. The Fallopian tubes and the uteri are covered and supported by a fold of the peritoneum called the broad ligament. The vagina passes dorsal to and between the two ureters to open below the bladder into the urinogenital canal, and this section of the tube which leads to the vulva is called the vestibule. The vulva is the urinogenital aperture. Its lips are called the labia majora, and the anterior angle is occupied by a rudimentary penis, called the clitoris.

It is an interesting fact that the accessory organs of both sexes are produced during development, that sex is manifested later during development by the hypertrophy of the one and the atrophy of the other. Even in the adult, remnants are

preserved and frequently accentuated which further indicate this. In the male, between the vasa deferentia at their terminal ends in the urethra a uterus masculinus is practically always present in mammals as a remnant of the Müllerian duct, and sometimes the inner end of the Müllerian duct may be traced in close proximity to the epididymis. In the female, similarly the broad ligament presents in the neighbourhood of the ovary remnants of the Wolffian duct and of the vasa efferentia. This goes to show that at the early period the endocrines which provide the stimuli for the growth of the organs are at first indifferent, and later become specific with respect to sex.

Germ Cells.—The essential elements of the reproductive system are the germ cells. They appear sooner or later in development : sooner in animals which quickly resolve their relatively few cells by differentiation, and later in animals which are able to preserve for a longer period cells in an indifferent state. But whether they appear early or late, whether they first become visible to us in ectoderm, endoderm, or mesoderm, is of little importance, for they are from their first appearance separate entities which maintain a single-celled state in the soma. It has been convenient in dealing with the vertebrates to speak of them arising in the germinal ridge. The fact is, however, that they may be recognised outside the ridge and that they migrate into the ridge. Independent as they are, we thus see that they are attracted in the soma to a special region, and we have no hesitation in ascribing the attraction to some chemical substance secreted by the somatic cells of the region. The result is the formation of an ovary or a testis, or both.

In the ovary and in the testis the germ cells multiply, maintaining, however, their individuality and conducting themselves as Protozoa in a state of protection. No difference is manifested, as a rule, during this period of multiplication between the testis and the ovary. The result is the provision of a number of germ cells, a number which appears to be specific. No further change takes place except one of growth until the period of maturity, when two successive divisions take place, resulting respectively in the formation of ova and spermatozoa.

In the case of many aquatic animals, up to and including

many fishes and amphibians, the act of fertilisation takes place in the water. In the rest, and necessarily in terrestrial forms, it takes place internally and the sperms have to be transferred into the oviduct. Water is thus the medium through which the sperms find their way to the ovum in the former, to which they are chemically attracted. In such the tendency is to the production of large numbers of eggs and sperms, and the death rate especially affects the young stages. In the case of forms which have internally fertilised eggs the rule is that few eggs are fertilised, and the elimination is done, therefore, at the stage of germ cells. Moreover, it is obvious that they have never a free period.

When fertilisation takes place the protozoon phase gives place to the metazoon in which the cells remain united to form a more or less complex body. In other words, the soma of one generation contains the protozoon phase of the next.

The protozoon phase of the Metazoa is protected, so usually are the young stages of the metazoon phase. Protection may last, and usually does last, during life in the parasitic, and is given indirectly to the weak and the helpless. But in Metazoa which acquire adequate powers of movement, protection and the need for it are outgrown. This is paralleled by the relationship of aquatic life to currents. When young, aquatic animals can only drift with the currents or are denatant. With increase in size and power they become more and more contranatant.

After the period of multiplication of the germ cells the products are termed respectively spermogones and oogones. A period of rest follows, during which the elements undergo a change into primary spermocytes and oocytes and the metazoon attains maturity. It is during this period also that the metazoon provoked directly by the spermocytes or the oocytes, or through the mediation of the other cells which form the testes or ovaries, exhibits conspicuous growth changes, and may be compelled to migrate. The germ cells themselves undergo a change, the most important evidence of which appears when the cell divides after the rest period is finished in the first of the two maturing divisions. It is then found, and the fact appears to be a universal one, true of plants as well as animals, that the chromosomes are reduced to half

the number. The reduced condition of the nucleus is called the haploid and the normal number the diploid, and the condition is further indicated by stating the number of the haploid as n and the diploid as $2n$. The second division maintains the haploid condition of the chromosomes of the nucleus, and in the case of the male for each spermocyte four spermatids result. The three stages are termed spermocyte 1, spermocyte 2, spermatid. In the case of the oocyte the corresponding stages are called oocyte 1, oocyte 2, ovum; the division is very unequal, a large cell and a small one being produced. The small cells are extruded as polar bodies, and the resultant large cell is the matured egg cell. The spermatids are each converted into a spermatozoon. The fusion of the spermatozoon with the ovum, each having the haploid number of chromosomes, brings into the egg the normal or somatic diploid number, and the $2n$ condition characterises the divisions of the resulting metazoon and of the contained germ cells until the matured phase, and so on.

The fundamental change which takes place at the end of the history of the germ cells is evidently of great importance, but it is questionable if we completely understand the meaning. It is clear that it indicates some preparation for the fusion which is imminent, even although only one spermatozoon of countless numbers is successful in gaining entrance. Knowing that an egg may in appearance be very similar to the egg of a totally different metazoon, and yet bears within it the properties which determine not only the kind of animal which will be produced, but even individual peculiarities, it has been natural to correlate the changes with the fact of heredity. It is impossible to go into this and other subjects which are associated with it in such a work as this. It is sufficient to point out to the student the groundwork of the theoretical and experimental work, which has attained to a high degree of importance in recent years. The results are accumulating at such a rate that books are only a partial guide, and periodicals such as the 'Journal of Genetics' should be referred to. But while the importance of the work is recognised to the full, and without denying the chromosome

basis on which it is founded, the student is asked to observe that in the cell not only do the chromosomes divide, but the whole of the nucleus and the cytoplasm. Moreover, the fact of polarity is becoming recognised as a factor of importance. Orientation is marked in the Protozoa. It is not absent in the protozoon phase of the Metazoa.

INDEX

NOTE.—The references to the types under each heading are given, not alphabetically, but in systematic order.

Printed in England at THE BALLANTYNE PRESS
SPOTTISWOODE, BALLANTYNE & CO. LTD.
Colchester, London & Eton